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# TIDAL FLUSHING OF INTRACOASTAL BAYS

Ned P. Smith

*Harbor Branch Foundation, Inc. R.R. 1, Box 196, Fort Pierce, FL 33450*
Harbor Branch Foundation, Contribution No. 303

## ABSTRACT

A numerical model is derived which describes the flushing of a coastal bay through tidal exchanges with the adjacent continental shelf. An expression for the renewal of bay water as a function of the number of elapsed tidal cycles involves a series of binomial coefficients which is equal in length to the number of tidal cycles. The model describes temporal variability in bay salinity, or any other measure of water quality, and indicates an asymptotic approach to a final value equal to that characteristic of shelf waters. The model is applied to Corpus Christi Bay, along the central Texas Gulf coast, and to Sarasota Bay, on the Gulf coast of Florida. For tidal processes alone, and ignoring significant beat frequencies in the local tides, the model suggests that 50% of the water of Corpus Christi Bay will be renewed in from 155 to 1,400 tidal cycles, assuming 90% and 10% mixing of flood tide waters within the bay, respectively. It is concluded that meteorologically forced exchanges and, to a lesser extent, fresh water run-off are significant in supplementing the tidal flushing of Corpus Christi Bay and maintaining water quality. Model results suggest that tidal flushing is considerably more effective in Sarasota Bay. With 50% mixing of flood tide waters, half of the bay water will be renewed in 4 tidal cycles, and essentially all of the bay water will be replaced within 30 tidal cycles.

Accepted 24 March 1982

## INTRODUCTION

An understanding of tidal processes forms the basis of investigations of mixing within estuarine waters, the exchange of water between an estuary and the adjacent continental shelf, and hence the flushing and resulting water quality of an estuary. Sufficiently long time series have been obtained in recent years to provide information on the supplementary role of meteorological forcing (Weisberg 1976; Smith 1977, 1979; Elliott and Wang 1978), and results indicate that these effects can be significant, especially in coastal regions with characteristically low amplitude tides. But weather processes are no more dependable than they are predictable. At the very least, tidal processes provide a baseline value. During times of prolonged calm, tidal exchanges may provide the only means by which water quality in an estuarine system is maintained.

Tidal flushing can be quantified in any of several ways, depending upon which simplifying assumptions are justified in a particular estuarine setting. Early studies in drowned river valley type estuaries involved a tidal prism,

defined to be the volume of water contained between the high and low tide levels in an estuary. The assumption that this water mixed completely within the estuary on the flood tide resulted in a substantial underestimate of the flushing time. Thus, a modification of the tidal prism method was developed (Ketchum 1951) in which the estuary was segmented in such a way that the low tide volume of any segment was equal to the high tide volume of the adjacent segment on the landward side. Complete mixing was then assumed only within each segment. This approach has been used with some success in the Raritan and Thames Rivers (Dyer and Taylor 1973) and elsewhere. More recently, further modification of this method has resulted in the introduction of a dispersion coefficient (Wood 1979) and an ability to handle branching into two or more channels (Brown and Arellano 1981).

Lee and Rooth (1972) have discussed tidal flushing in coastal lagoons, with Biscayne Bay, Florida, as an example. A tidal mixing time scale is suggested which is directly proportional to the basin length and inversely proportional to the water depth and the maximum tidal current speed. The approach appears to be realistic in estuarine basins which are broad, shallow and greatly elongated.

The formulation of a model for tidal flushing of an intracoastal bay must reflect the shape and circulation that characterizes this type of estuary. An intracoastal bay has a more circular shape, and the net flow is usually two-dimensional, and is formed into one or more gyres. Ward (1980) has discussed several examples of Gulf coast bays in which the circulation is dominated by persistent, wind-driven gyres. Significant tidal motions may be restricted to a relatively small portion of the bay in the immediate vicinity of the channel connecting the bay with the waters of the inner shelf. In an estuarine setting such as this, it is inappropriate to define adjacent segments which exchange water with each complete tidal cycle. Rather, tidal flushing involves a more complex interaction of tidal oscillations and slowly rotating gyres. A fraction of the water flooding into the bay will be removed intact at the start of the ebb; only water entering the bay sufficiently early in the flood cycle will be caught up in the internal circulation of the bay and retained. This may indeed mix completely with time, but it will not be water of this mixture that leaves the bay on the following ebb. Rather, water exported to the shelf will be that brought past the outlet by the appropriate gyre during the ebb cycle. The hydrographic properties of that water will be a reflection of mixing that has been in progress over several previous tidal cycles.

The purpose of this study was to consider tidal flushing within a framework of assumptions and physical conditions appropriate for a coastal bay, and to develop a numerical model appropriate for estimating baseline flushing times in response to tidal processes alone. Simulations of temporal changes in hydrographic properties indicate a quasi-exponential response within the bay, with concentrations of dissolved material asymptotically approaching a value which is assumed constant in shelf waters. The model is applied to Corpus Christi Bay, Texas, and Sarasota Bay, Florida, to provide examples of slow and rapid tidal flushing, respectively. Finally, tidal flushing

is discussed in terms of beat frequencies and nontidal processes characteristic of these two bays.

## THE MODEL

Consider an intracoastal bay with a low tide volume $V_\circ$ and an initial salinity $S_\circ$. On the first flood tide, a volume of water (the tidal prism) $v$ enters from the inner shelf with salinity $S'$. A fraction, $n$, of $v$ mixes with $V_\circ$; the rest leaves on the following ebb, along with a volume, $nv$, of the original bay water, and the volume of the bay returns to $V_\circ$. The salt content of the bay after one tidal cycle, $V_\circ S_1$, will be the original salt content, $V_\circ S_\circ$, corrected for the gain and loss during the flood and ebb cycles, respectively:

$$V_\circ S_1 = V_\circ S_\circ + nvS' - nvS_\circ$$

If we define an effective tidal prism, $\varepsilon$, as that fraction of the tidal prism which remains in the bay, $nv$, the above expression reduces to

$$V_\circ S_1 = V_\circ S_\circ + \varepsilon\,(S' - S_\circ).$$

Thus, the salinity of the bay after one tidal cycle is

$$S_1 = V_\circ S_1/V_\circ = S_\circ + (\varepsilon/V_\circ)\,(S' - S_\circ)$$

We assume that through mixing within the bay the salt entering from the shelf is distributed uniformly before the next tidal cycle. This is clearly an oversimplification, but it is necessary if one is to avoid making assumptions regarding the salinity distribution within the bay. For convenience, we define $\Delta S$ to be the difference between the original bay salinity and that of shelf waters: $\Delta S = S' - S_\circ$. Continuing, we find that at the end of the second tidal cycle

$$\begin{aligned} V_\circ S_2 &= V_\circ S_1 + \varepsilon S' - \varepsilon S_1 \\ &= (V_\circ - \varepsilon)\,S_1 + \varepsilon S'. \end{aligned}$$

But, from above, $S_1 = S_\circ + \Delta S\,(\varepsilon/V_\circ)$. Substituting and simplifying, we get

$$V_\circ S_2 = V_\circ S_\circ + \Delta S[(2\varepsilon - (\varepsilon^2/V_\circ)],$$

and thus the salinity after two tidal cycles is

$$S_2 = S_\circ + \Delta S[(2\varepsilon/V_\circ) - (\varepsilon^2/V_\circ^2)].$$

If we define $\eta$ to be the ratio of the effective tidal prism, $\varepsilon$, to the low water volume of the bay, $\eta = \varepsilon/V_\circ$, then after three tidal cycles

$$S_3 = S_\circ + \Delta S\,(3\eta - 3\eta^2 + \eta^3).$$

For the fourth tidal cycle:

$$\begin{aligned} S_4 &= S_\circ + \Delta S[4\eta - 6\eta^2 + 4\eta^3 - \eta^4], \\ &= S' - \Delta S[1 - 4\eta + 6\eta^2 - 4\eta^3 + \eta^4] \end{aligned}$$

It is apparent that in this last form the coefficients in the bracketed term are the binomial coefficients. Specifically, the $m^{\text{th}}$ coefficient for the $n^{\text{th}}$ tidal cycle is given by

$$\binom{n}{m} = n!/(n - m)\,!\,m!,$$

and the general expression for bay salinity after $n$ tidal cycles is

$$S_n = S' - \Delta S \sum_{m=0}^{n} \binom{n}{m} (-\eta)^m. \tag{1}$$

Because the effective tidal prism can be quite small relative to the total volume of the bay, many tidal cycles may have to be considered before a significant fraction of the bay is flushed by tidal processes. This presents computational difficulties, since $n!$ becomes too large to be handled by many computing systems for calculations corresponding to time intervals on the order of a month (with predominantly diurnal tides). The DEC PDP 11/34 computer used in this study could not simulate tidal flushing for more than 32 tidal cycles. Thus, calculations were carried out in groups of ten tidal cycles, with the resulting bay-shelf salinity differences after any ten cycles serving as a new $\triangle S$ for the next ten-cycle calculation.

## APPLICATION OF THE MODEL

The numerical model can be applied to any intracoastal bay for which the effective tidal prism, the low-tide volume and the degree of mixing within the bay is either known or can be estimated. Here, the model is used to investigate tidal flushing in Corpus Christi Bay, in the northwestern corner of the Gulf of Mexico (Fig. 1), and Sarasota Bay, along the Gulf coast of Florida (Fig. 2). Together, these two bays represent opposite extremes in terms of the effectiveness of tidal flushing. Tidal conditions in Sarasota Bay have not been quantified particularly well, but available information is adequate to suggest that tidal flushing is considerably more efficient in this bay than in Corpus Christi Bay.

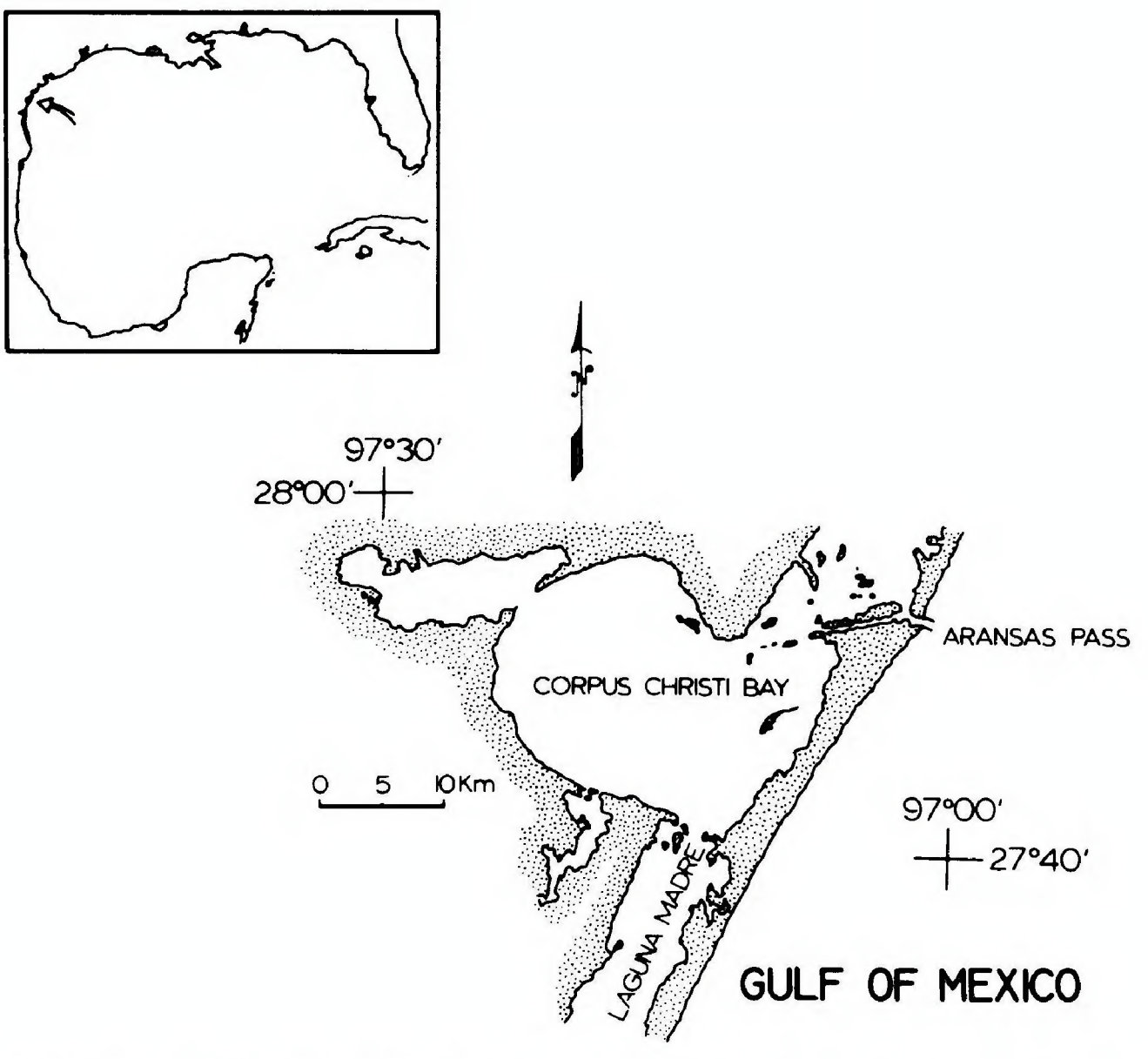


FIG. 1. Corpus Christi Bay and the Aransas Pass. Arrow in insert map shows the location of the study area along the central Texas Gulf coast in the northwestern Gulf of Mexico.

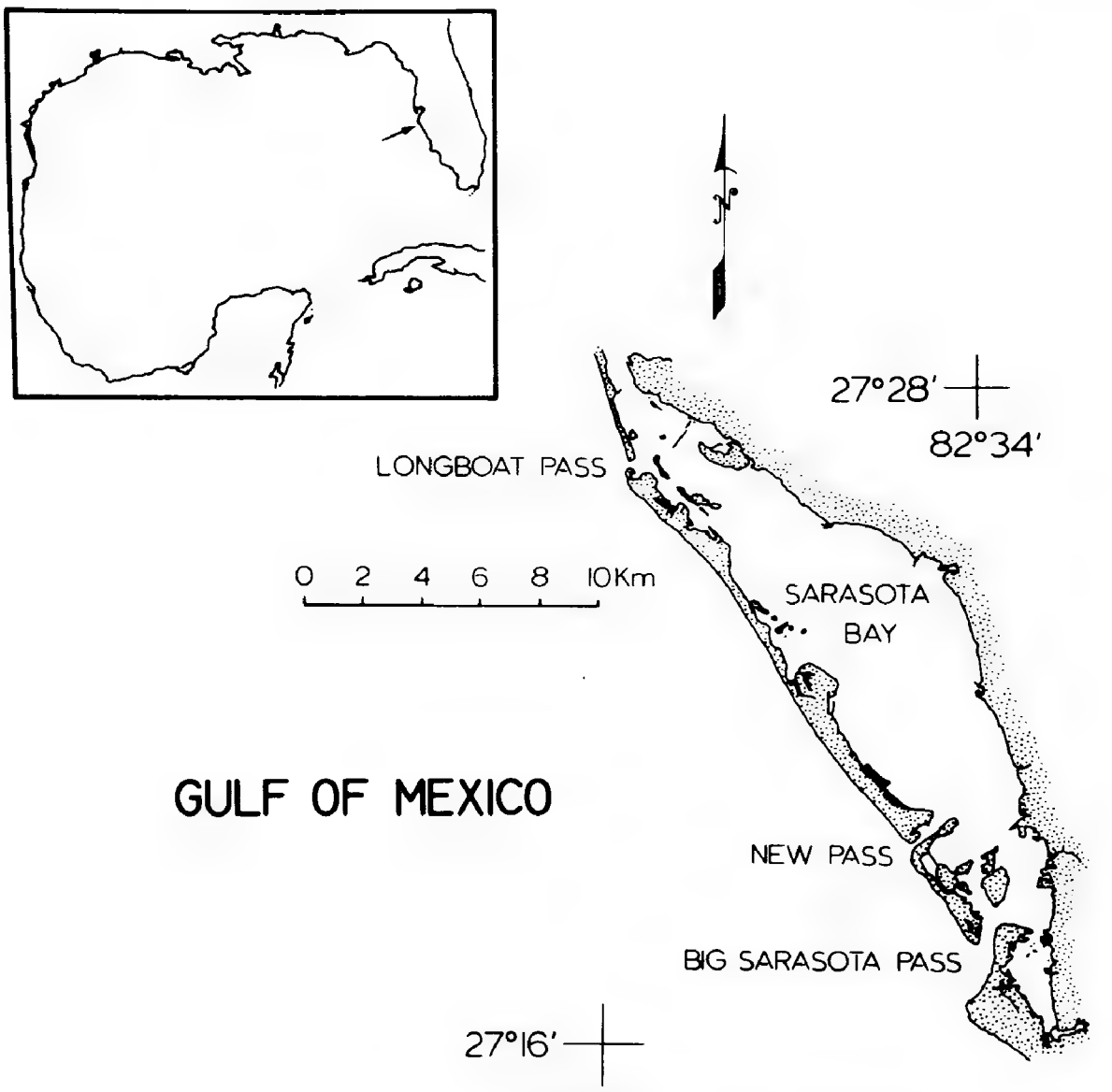


FIG. 2. Sarasota Bay and connecting passes. Arrow in the insert map shows the location of the study area along the Gulf coast of Florida in the eastern Gulf of Mexico.

## A. Corpus Christi Bay, Texas

Previous work done in Corpus Christi Bay (Smith 1977) provides some of the values needed to run the model over an appropriate range of tidal cycles. At the same time, the physical setting of the bay is well suited for illustrating some of the difficulties that may arise with the application of the model to certain situations. The bay is approximately circular, with east-west and north-south dimensions of about 26 and 20 km, respectively. The surface area of the bay is approximately 297 $km^2$, and mid bay depths are on the order of 3.5 m. Collier and Hedgpeth (1950) have estimated the mean low water volume of Corpus Christi Bay to be $1{,}143 \times 10^6$ $m^3$. It is noteworthy that the bay is connected to the Gulf of Mexico by a dredged ship channel which itself contains approximately $37 \times 10^6$ $m^3$ of water.

Tides along the northwestern rim of the Gulf of Mexico are mixed but principally diurnal, with a form number of 2.5 at the Aransas Pass jetties, and over 6.0 in the bay itself (Smith 1974). The tidal range in the bay varies from a few centimeters at times of equatorial tides to as much as 30 cm during tropic tides. A harmonic analysis of the hour-by-hour variation of the bay surface above a reference datum (Smith 1977) quantified the tidal prism associated with each of the principal tidal constituents. Here, we shall work initially with a single, hypothetical tidal constituent which has the same long-term effect as the several principal tidal constituents working in concert. Later, we shall discuss the effect of the fortnightly tidal cycles in flushing the bay.

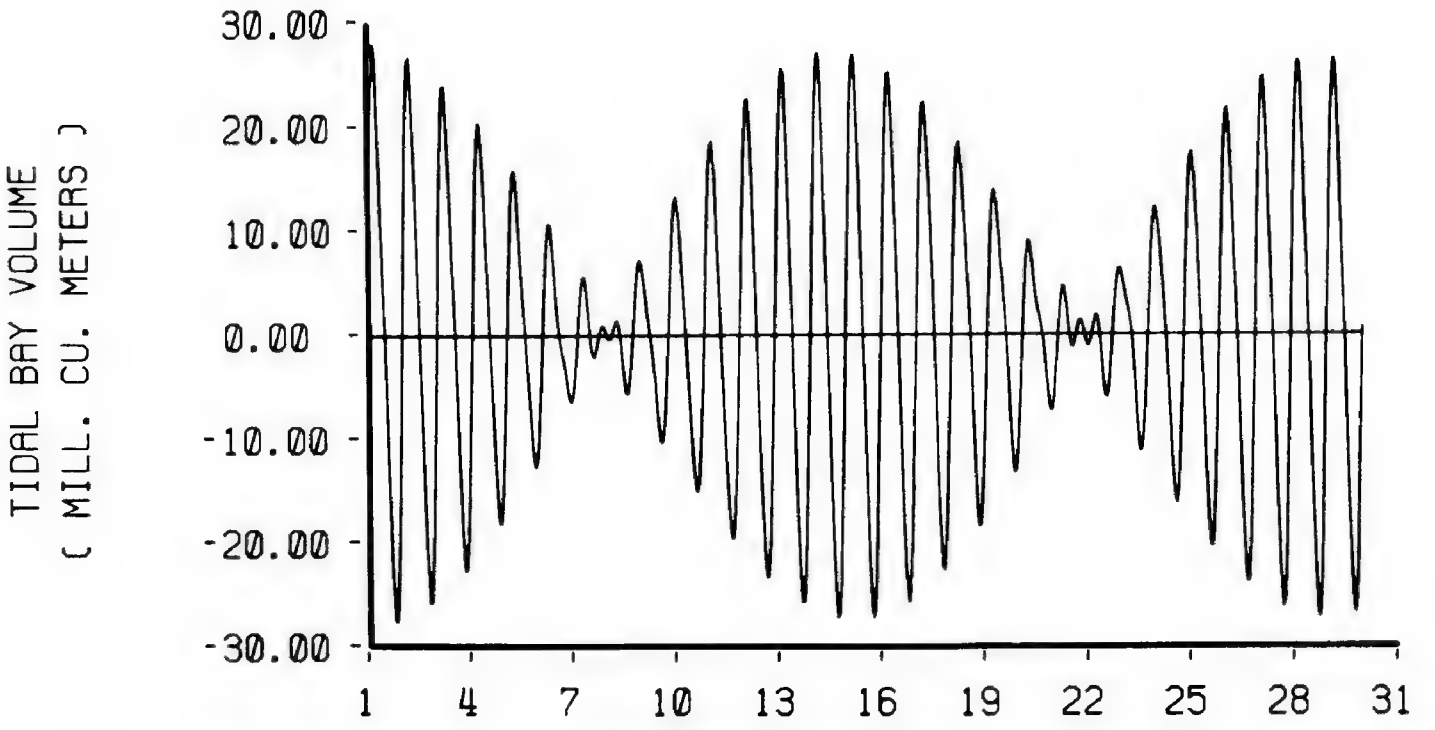


FIG. 3. Time-plot of the volume of Corpus Christi Bay varying in response to tidal exchanges only. Amplitudes were taken from Smith (1977); local phase angles were not incorporated into the calculations. Horizontal axis is time in days.

Figure 3 shows the temporal variation in bay volume due to tidal processes alone. The curve was constructed from the sine waves representing the five major tidal constituents ($K_1$, $O_1$, $P_1$, $M_2$ and $S_2$). Phase angles were not incorporated into the calculations. Because of the ship channel, only tidal exchanges involving more than 37.3 x $10^6$ $m^3$ of water will move water from the bay to the inner shelf of the Gulf, or vice versa. Thus, over a 29-day synodic month, water originating over the inner shelf moves into the bay on the flood tide only in bursts of 6-8 successive tidal cycles, during tropic tide conditions. The tidal prism during equatorial tides is less than the volume contained in the ship channel. Thus, at these times, channel water at the start of the flood must be bay water which had left on the preceding ebb, and its return to the bay does not constitute a flushing action. Integrating under the tidal curve only outside the limits of $\pm$18.65 x $10^6$ $m^3$, one finds that there is never more than 19.2 x $10^6$ $m^3$ brought into the bay on any given tidal cycle. From calculations made to construct Figure 3, a total of 163.7 x 7 x $10^6$ $m^3$ of Gulf water entered the bay, at least temporarily, on 14 tidal cycles during this 29-day period. This is equivalent to 5.64 x $10^6$ $m^3$ per tidal cycle, and thus for model calculations we let $v$ = 5.64 x $10^6$ $m^3$, and $\eta = \varepsilon/V_\circ = 0.00404\, n$, where $n$ is the fraction of the tidal prism remaining in the bay.

The percentage of the tidal prism actually exchanged in Corpus Christi Bay on any given tidal cycle is an unknown entity. We therefore proceed using three values, which represent assumptions of 10%, 50% and 90% mixing. Values for $\eta$ then become 0.000404, 0.00247 and 0.00444, respectively. Using these three values to represent the extremes of tidal flushing and to provide a representative value for comparison with Sarasota Bay, a family of curves can be constructed from repetitive calculations of Equation 1 (Fig. 4). These curves describe the quasi-exponential renewal of bay water from an initial state to a final state equal to that of shelf waters.

The calculations are carried out over 1000 tidal cycles, corresponding in time to over 2.5 years, in view of the dominance of the diurnal tidal constituents in the bay. We note in particular the number of tidal cycles required to renew 50% of the initial bay water. Logically, this varies with the degree of mixing assumed per tidal cycle, however the difference calculated for the selected extremes of 10% and 90% is dramatic. If 90% of the water entering the bay on the flood tide is caught up in a gyre, or otherwise mixed and retained within the bay, 155 tidal cycles

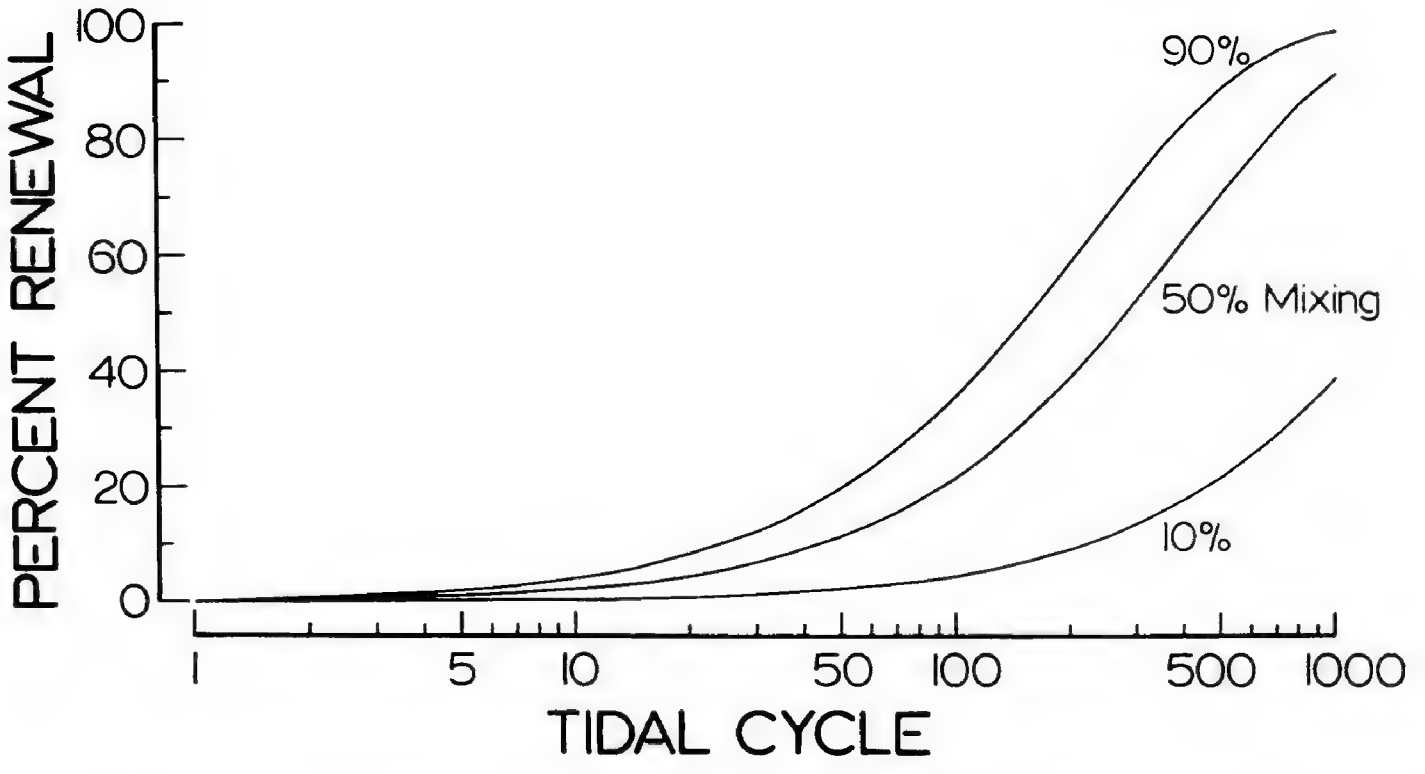


FIG. 4. Composite of curves showing the renewal of Corpus Christi Bay water as a function of elapsed tidal cycles, assuming 10%, 50% and 90% mixing of flood tide water within the bay.

would be required to remove 50% of the original low tide water and decrease by half the original bay-shelf salinity difference. If only 10% of the flood water remains in the bay, 1400 tidal cycles would be needed to produce the same effect. The 50% mixing curve, which may be the best estimate until the necessary hydrographic data become available, passes through the 50% renewal level on the 280th tidal cycle, corresponding to approximately 9 months in time.

## B. Sarasota Bay, Florida

The second application of the model produces results of quite a different kind. Sarasota Bay, on the Gulf coast of Florida, is about half the size of Corpus Christi Bay, with a surface area of 141 $km^2$. Mid bay depths are approximately 3.5 m, but there are extensive shallow areas around the fringe, and thus the low tide volume of the bay is only 143 x $10^6$ $m^3$ (McNulty, *et al.* 1972).

Tidal measurements are not available from within the bay. However tidal conditions can be approximated with harmonic constants from a one-year water level record obtained at Anna Marie, 12 km north of Longboat Pass (Zetler and Hansen 1970). Tides are mixed, with a form number of 1.5. There is a strong diurnal signal, but it is modulated greatly (Fig. 5), and tidal ranges during tropic tide conditions are approximately 5 times those during equatorial tides. The maximum diurnal tidal range is 0.67 m. A single, hypothetical tidal constituent with an amplitude of 0.21 m was used to quantify the tidal prism. The variance of a single sine wave with an amplitude of 0.21 m was equal to that calculated from the data used to plot Figure 5, and therefore its effect on tidal flushing of the bay is similar. The mean tidal prism was determined to be approximately 57.4 x $10^6$ $m^3$, or about 32% of the low tide volume of the bay. The three passes connecting the bay with the Gulf of Mexico are short, and it is therefore probable that most of the water comprising the tidal prism in the bay originates in the Gulf, rather than in one of the connecting channels. Thus, a value of $\eta = 0.1593\, n$ was used in the calculations.

Assuming again that 50% of the water arriving from the Gulf mixes within the bay, the model suggests that half of the water in the bay is renewed by the end of the fourth tidal cycle (of mean diurnal range), and essentially all of the water of Sarasota Bay is replaced within 30 tidal cycles. A plot of renewal percentage as a function of elapsed tidal cycles is not presented, due to uncertainties surrounding the magnitudes of the tidal prisms associated with the major constituents for the bay. Thus, a confirmation of these results awaits better water level records. But one may conclude tentatively from the crude calculations presented here that tidal flushing is rapid and efficient in renewing the water of this estuarine system.

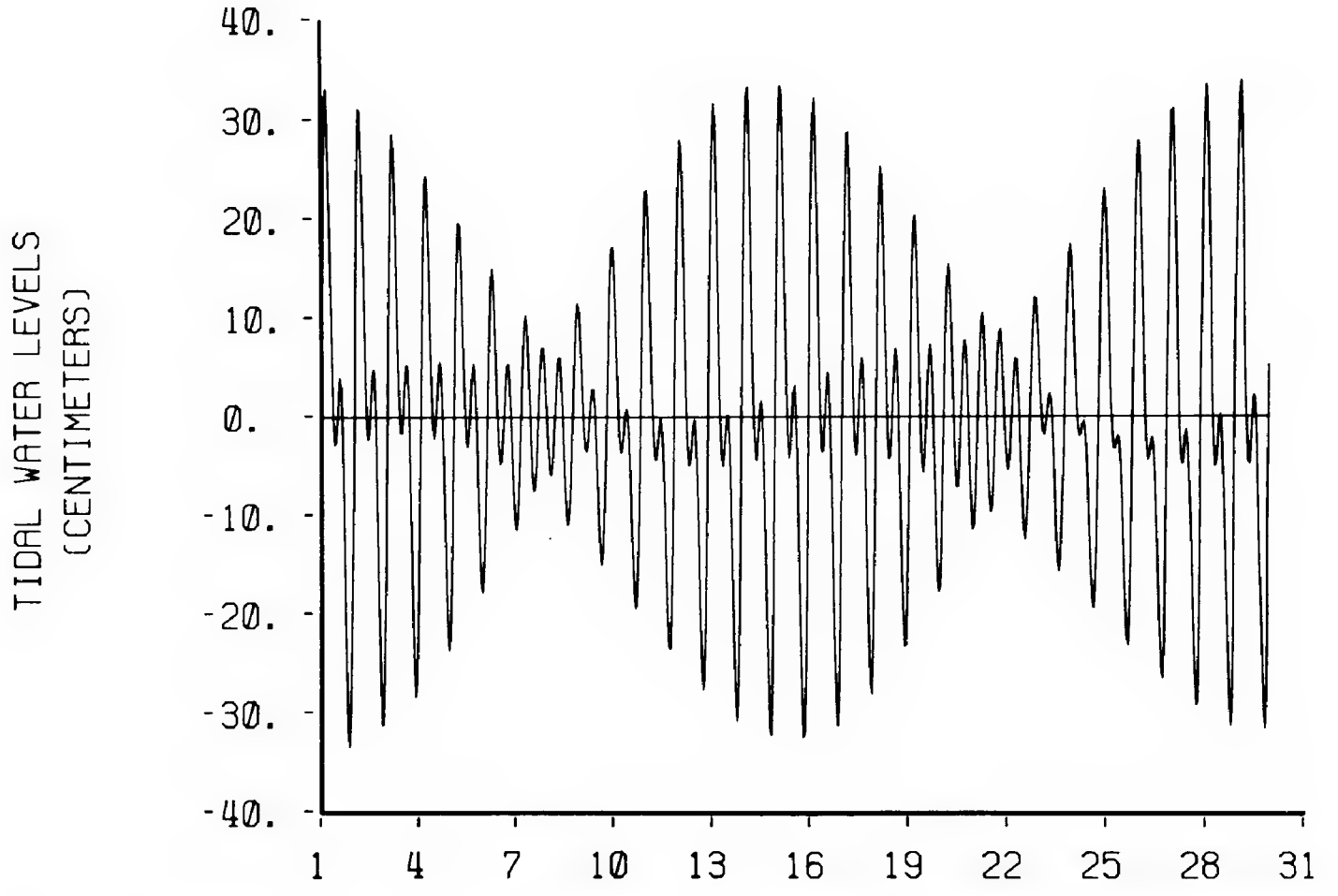


FIG. 5. Time-plot of water levels for Sarasota Bay varying in response to tidal exchanges only. Amplitudes were taken from Zetler and Hansen (1970) for Anna Marie, and scaled down to maximum diurnal ranges reported by McNulty, *et al.* (1972). Local phase angles were not incorporated into the calculations. Horizontal axis is time in days.

## DISCUSSION

The time-plot of tidal bay volume (Fig. 3) is useful for putting the tidal flushing of Corpus Christi Bay in a proper perspective. Specifically, as a result of the fortnightly beat frequency of the dominant $K_1$ and $O_1$ tidal constituents, tidal flushing takes on a cyclical behavior, and there are periods of 8-9 days during which little or no water from the Gulf enters the bay, or vice versa. Rather, the co-oscillating tidal motions result in bay or Gulf water being stored temporarily in the channel before returning to its place of origin during the last half of the tidal cycle. In this physical setting, then, tidal flushing appears to occur in bursts. The situation is similar for Sarasota Bay, though with no long channels connecting the inner shelf with the bay, it is probable that at least some flushing occurs on each tidal cycle. Effects are still highly variable, however, over a synodic month. The effect of a mixed tide has received little attention in discussions of tidal flushing in estuaries.

A thorough treatment of tidal flushing must touch at least briefly on the supplementary role played by meteorological forcing. Here we must focus upon Corpus Christi Bay, as little work of this type has been conducted in Sarasota Bay. The central Texas Gulf coast is a region of characteristically

strong winds. The International Airport at Corpus Christi is listed by the National Weather Service as the third windiest airport in the country, with a scalar wind speed averaging 24.3 km/h. Both windstress (Smith 1977) and variations in atmospheric pressure (Smith 1979) are capable of producing bay-shelf exchanges equal in importance to all but the principal tidal constituents. In one instance, the rapid reversal and increase in windstress associated with a frontal passage in February, 1972, removed approximately 10% of the volume of the bay in a period of 56 hours. The renewal rates given in the preceding section therefore represent a baseline (minimum) value, which may in fact be enhanced substantially even by unexceptional meteorological events. It is probable that the degree of mixing associated with the slower filling and draining by meteorological forcing may be greater, since there is more time available for water to be caught up in the internal circulation of the bay.

Another source of flushing is the fresh water entering the bay, moving through in one or more gyres (perhaps maintaining some of the semi-permanent features of bay circulation by creating barotropic or baroclinic pressure gradients within the bay), and finally being exported onto the continental shelf. In the case of Corpus Christi Bay, the multi-annual mean fresh water influx was found to be 20.6 $m^3/s$ over the period 1951-1968 (Diener 1975). With a surface area of 297 $km^2$, an excess evaporation over precipitation of 0.59 cm/day would be required to remove all this fresh water from the bay before it moved through and out onto the shelf. It is noteworthy in this regard that Smith (1981) has calculated an evaporation rate of 0.19 cm/day from the surface of upper Laguna Madre, immediately south of Corpus Christi Bay (Fig. 1), during a 68-day study in the winter of 1973–74. The excess evaporation over precipitation during this time was 0.08 cm/day. This value is in good agreement with calculations based upon climatological maps for the Texas coastal zone (Texas General Land Office 1975, Arbingast, *et al.* 1976). Evaporation from the bay surface is estimated to exceed direct precipitation by anywhere from 46-74 cm/year, which is equivalent to 0.13–0.20 cm/day.

This appears to leave a significant fraction of the fresh water entering the bay available for a flushing role. In fact, if three-fourths of the fresh water entering the bay moves through and out onto the shelf without evaporating, 856 days would be needed to displace 50% of the bay water. For comparison, the model predicts that 856 tidal cycles would renew 88% of the bay water, assuming 50% mixing of the flood tide (Fig. 4). Thus, ignoring the nature of the movement of fresh water through the bay, one may tentatively conclude that flushing by fresh water is significant, but, on the average, it appears to play a secondary role to tidal exchanges in this physical setting.

The average fresh water inflow, however, may not be a particularly good measure of fresh water inflow at a given time. This is especially true along the central Texas Gulf coast, where normally semi-arid conditions can give way to temporarily heavy rains. This "flashiness" in fresh water run-off generally occurs over time scales on the order of a few days to perhaps a

week, but some values from the U.S. Geological Survey stream gage on the Nueces River (Diener 1975) are noteworthy. Ignoring hurricane-related rains, which constitute an extreme case, mean monthly discharges in April and May, 1968, were 2.9 $m^3/s$ and 124 $m^3/s$, respectively. The effect of excessive fresh water inflow is to create both a barotropic and a baroclinic pressure gradient. The former aids the ebbing of water out of the bay; the latter enhances mixing of water within the bay. Rapid changes of fresh water discharge occur in Sarasota Bay as well, but they are less extreme. Furthermore, because the drainage area of the principal tributary (Phillipi Creek) is only 62 $km^2$, and mean monthly discharge rates are generally between 0.1 and 1.9 $m^3/s$, the effects of even extreme flow rates would be relatively small.

The rather lengthy time intervals postulated for the renewal of water in Corpus Christi Bay by tidal exchanges and the mean fresh water runoff implies that exchanges in response to meteorological and hydrologic events must be dominant—if the bay is well flushed. It would appear that the bay is in fact well flushed, since bay-shelf salinity differences are on the average negligible, while the sum of direct precipitation and runoff is on the order of 4-6 times greater than evaporation. The mean salinity of bay water samples taken between 1964 and 1968 was found to be approximately 31.4 parts per thousand (ppt) (Smith 1978). Surface samples from a station 14 km offshore during 1976 and 1977 were found to average 31.5 ppt (Smith 1980). Behrens (1966) has documented long-period salinity cycles in Texas intracoastal waters, extending over time scales of several years. Thus, while a comparison of mean bay and shelf salinities computed from different time intervals is not strictly valid, the available information suggests that on the average the difference in the salinity of bay and shelf waters is kept to a minimum. This implies that there is a relatively active exchange of water, presumably in response to discrete events.

It is important to note that the development of the model in terms of salinity does not restrict its application to other indicators of water quality, or to any conservative hydrographic variable. Thus, the half-life of any dissolved or suspended substance for which bay-shelf differences exist would seem to be on the order of 9 months for Corpus Christi Bay, and several days (depending upon tidal conditions) for Sarasota Bay—when only tidal processes are considered. These time estimates can change appreciably, of course, when information becomes available to suggest that mixing of flood tide waters differs significantly from the 50% value used here for comparison purposes.

Any numerical model of tidal flushing is bound to involve simplifying assumptions of one sort or another to facilitate the evaluation of the appropriate equations. In this case, aside from the substitution of one hypothetical tidal constituent for the several major constituents which combine to produce the distinct beat frequencies, the assumption that the net salt flux into the bay on any given tidal cycle is uniformly distributed throughout the bay prior to the next tidal cycle is clearly compromising

reality. Three years of hydrographic data from Corpus Christi Bay (Holland *et al.* 1975) show that significant horizontal gradients may exist at any time of year. Furthermore, to the extent that gyres dominate the internal circulation of the bay, there may exist isolated regions which are little affected by tidal flushing. Refinements to the simple techniques presented here can be incorporated when the hydrography and dynamics of coastal bays are understood better.

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## LITERATURE CITED

ARBINGAST, S. A., L. G. KENNAMER, R. H. RYAN, J. R. BUCHANAN, W. L. HEZLEP, L. T. ELLIS, T. G. JORDAN, C. T. GRANGER and C. P. ZLATKOVICH. 1976. *Atlas of Texas.* The Univ. of Texas, Bureau of Business Research. 179pp.

BEHRENS, E. W. 1966. Surface salinities for Baffin Bay and Laguna Madre, Texas, April 1964–March 1966. *Publications of the Institute of Marine Science, University of Texas.* **11**:168–173.

BROWN, W. S. and E. ARELLANO. 1981. The application of a segmented tidal mixing model to the Great Bay Estuary, N. H. *Estuaries.* 3:248–257.

COLLIER, A. and J. W. HEDGPETH. 1950. An introduction to the hydrography of tidal waters of Texas. *Publications of the Institute of Marine Science, University of Texas.* 1(2):121–194.

DIENER, R. A. 1975. Cooperative Gulf of Mexico estuarine inventory and study—Texas: area description. *NOAA Technical Report NMFS CIRC*–393. 129pp.

DYER, K. R. and P. A. Taylor. 1973. A simple segmented prism model of tidal mixing in well-mixed estuaries. *Estuarine and Coastal Marine Science.* 1:411–418.

ELLIOTT, A. J. and D-P WANG. 1978. The effect of meteorological forcing on the Chesapeake Bay: the coupling between an estuarine system and its adjacent coastal waters. pp. 127–146. In J. C. J. Nihoul (Ed.) *Hydrodynamics of Estuaries and Fjords.* Elsevier Scien. Publ. Co., Amsterdam.

HOLLAND, J. S., N. MACIOLEK, R. KALKE, L. MULLINS and C. H. OPPENHEIMER. 1975. A benthos and plankton study of the Corpus Christi, Copano and Aransas Bay systems. Third Year Rept., Univ. of Texas Marine Science Inst., 174 pp.

KETCHUM, B. H. 1951. The exchanges of fresh and salt waters in tidal estuaries. *Journal of Marine Research.* 10:18–38.

LEE T. H. and C. ROOTH. 1972. Exchange processes in shallow estuaries. Proceedings, Offshore Technol. Conf., May 1972, Paper ETOC 1703, 12 pp.

McNULTY, J. K., W. N. LINDALL and J. E. SYKES. 1972. Cooperative Gulf of Mexico estuarine inventory and study, Florida: Phase I, Area Description. *NOAA Technical Report NMFS CIRC*–368, 126pp.

SMITH, N. P. 1974. Intracoastal tides of Corpus Christi Bay, *Contributions in Marine Science.* 18:205–219.

_____. 1977. Meteorological and tidal exchanges between Corpus Christi Bay, Texas, and the northwestern Gulf of Mexico. *Estuarine and Coastal Marine Science.* 5:511–520.

_____. 1978. Tidal and long-period exchanges between upper Laguna Madre and Corpus Christi Bay, Texas. *TAIUS, Texas A & I University Studies.* 11:39–51.

_____. 1979. Meteorological forcing of coastal waters by the inverse barometer effect. *Estuarine and Coastal Marine Science.* 8:149–156.

———. 1980. On the hydrography of shelf waters off the central Texas Gulf coast. *Journal of Physical Oceanography.* 10:806–813.

———. 1981. Energy balance in a shallow seagrass flat for winter conditions. *Limnology and Oceanography.* 26:482–491.

TEXAS GENERAL LAND OFFICE. 1975. Physiography and Climate Map, Plate 1A, Upper Texas Coastal Region. Coastal Management Program, Austin, Texas.

WARD, G. H. 1980. Hydrography and circulation processes of Gulf estuaries. 183–215. In P. Hamilton and K. MacDonald, (Eds.) *Estuarine and Wetland Processes.* Plenum Publ. Co., New York.

WEISBERG, R. H. 1976. A note on estuarine mean flow estimation. *Journal of Marine Research.* 34:387–394.

WOOD, T. 1979. A modification of existing simple segmented tidal prism models of mixing in estuaries. *Estuarine and Coastal Marine Science.* 8:339–347.

ZETLER, B. and D. V. HANSEN. 1970. Tides in the Gulf of Mexico—a review and a proposed program. *Bulletin of Marine Science.* 20:57–69.

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# SPATIAL AND SEASONAL DISTRIBUTION OF HYDROCARBON-UTILIZING BACTERIA OF SEDIMENT FROM THE NORTHWESTERN GULF OF MEXICO

Steve K. Alexander, Steven J. Schropp, and John R. Schwarz

*Department of Marine Biology, Texas A&M University at Galveston, Galveston, Texas 77553*

## ABSTRACT

Hydrocarbon-utilizing bacteria were enumerated in sediment collected seasonally from four sites representative of offshore, nearshore, and estuarine environments of the northwestern Gulf of Mexico. Hydrocarbon utilizers, enumerated in a basal-oil medium using the most-probable-number (MPN) method, were detected in 438 of 448 samples in numbers that ranged from $8.0 \times 10^1$ to $1.1 \times 10^6$ per ml wet sediment. The total viable heterotrophic population in 70% of the sediment samples contained less than 2% hydrocarbon utilizers. Analysis of spatial variations revealed that populations were most abundant in estuarine sediment and decreased with increasing distance from shore. Significant seasonal differences were observed at all four sites, with highest numbers in summer or fall. Spatial variations in population levels may be related to hydrocarbon input, while seasonal changes may be controlled primarily by temperature. Results from the present study indicate that sediments from the northwestern Gulf of Mexico contain a dynamic resident population of bacteria capable of utilizing hydrocarbons.

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## INTRODUCTION

Hydrocarbon-utilizing bacteria can remove large quantities of oil from the marine environment (Floodgate 1972). Surveys of hydrocarbon utilizers, therefore, are an integral part in assessing the fate of oil that enters an ocean area. Such studies have been conducted in several ocean regions prior to extensive oil development (Gunkel 1973; Mulkins-Phillips and Stewart 1974; Oppenheimer *et al.* 1980; Roubal and Atlas 1978). In addition to indicating oil degradative potential, concentrations of hydrocarbon utilizers may also be a useful indicator of the degree of oil pollution (Atlas and Bartha 1973; Hood *et al.* 1975; Walker and Colwell 1973).

The Gulf of Mexico is one of the most intensive oil-producing areas in the world and is a heavily traveled tanker route (Geyer 1980). These activities create the potential for both chronic and catastrophic input of oil into this

system. Therefore, surveys of hydrocarbon-utilizing bacteria are an essential aspect of environmental assessment in this ocean region. However, few surveys have been conducted in the Gulf of Mexico (Brown *et al.* 1980; Crow *et al.* 1975; Oujesky *et al.* 1979; Zobell and Prokop 1966).

In the present study, sediment was collected seasonally from four sites representative of offshore, nearshore, and estuarine environments of the northwestern Gulf of Mexico. The primary objectives of the study were to: 1) evaluate the presence and abundance of hydrocarbon-utilizing bacteria; and 2) determine their spatial and seasonal distribution. This study represents the first large-scale survey of hydrocarbon-utilizing bacteria of sediment from this region of the Gulf of Mexico.

## MATERIALS AND METHODS

Sediment was collected from offshore, nearshore, and estuarine environments of the northwestern Gulf of Mexico (Fig. 1). Offshore site samples were collected from 12 stations

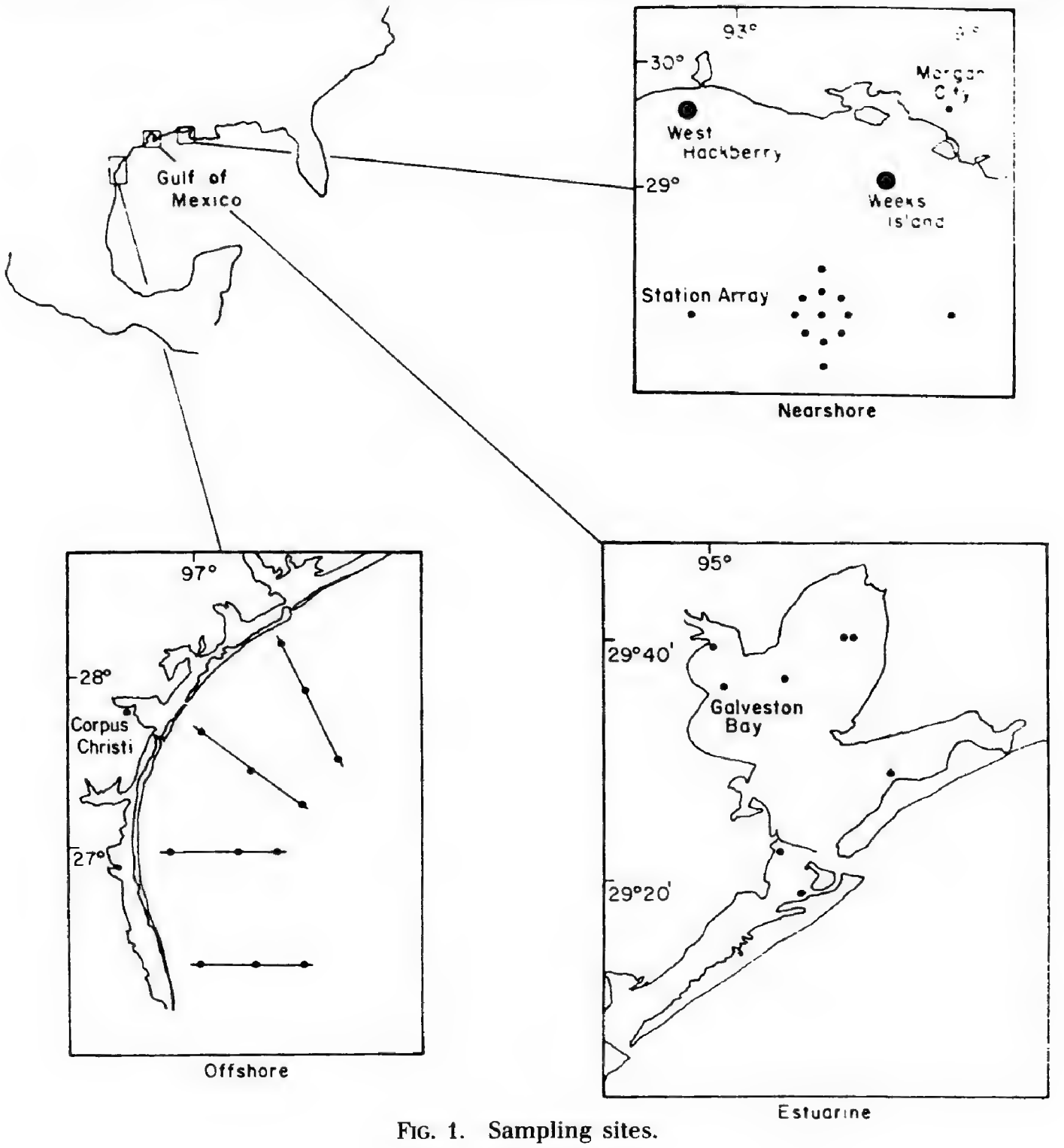


FIG. 1. Sampling sites.

located along four transects on the south Texas outer continental shelf. Nearshore collections were from two sites off Louisiana, West Hackberry and Weeks Island. Thirteen stations were sampled at each nearshore site. Estuarine site collections were from eight stations located in shallow, open-water areas of the Galveston Bay system of Texas. Offshore collections were made in March, June, and October of 1977. Nearshore samples were collected in June and October of 1978, and in January and May of 1979. Estuarine collections were in July and October of 1978, and in January and June of 1979.

Various grab samplers were used for sediment collection: a Smith-McIntyre grab was used offshore, a Van Veen grab nearshore, and an Ekman grab at estuarine stations. The top 1-2 cm of sediment was removed from the grab with a spatula and placed into a sterile container. Samples were stored on ice until processing, usually within several hours of collection.

Field sampling variables monitored at each station during the study included: station depth, sediment temperature (mercury-filled glass thermometer), water salinity (Goldberg T/C refractometer, American Optical Corp., Buffalo, N.Y.), and total viable heterotrophic bacteria. Serial dilutions of sediment in volumes of 0.1 ml were spread-plated in triplicate onto Marine Agar 2216 (Difco Laboratories). The inoculated plates were incubated at the seasonal *in situ* temperature for 10 days before bacterial colony enumeration.

Hydrocarbon-utilizing bacteria were enumerated in a basal-oil medium by the most-probable-number (MPN) method. This method is superior to solid media for estimating microbial populations with specific degradative capabilities (Colwell 1979). Duplicate (south Texas, Galveston Bay) or triplicate (nearshore sites) sediment samples from each station were serially diluted in sterile artificial seawater (Instant Ocean) and 1 ml of four sediment dilutions were inoculated into tubes (three per dilution) containing 10 ml of basal medium and 0.05 ml autoclaved south Louisiana crude oil. The basal medium consisted of 1 g $NH_4NO_3$ and 1 g $KH_2PO_4$ per liter of artificial seawater. The pH of the medium was adjusted to 7.6 by the addition of 1 N NaOH prior to use. After inoculation, tubes were incubated in a stationary position for 30 days at the seasonal *in situ* temperature. Positive tubes were determined by visual inspection, i.e. presence of pellicle, turbidity, and changes in the appearance of oil. Pellicle formation on the medium surface in the majority of positive tubes precluded the use of a spectrophotometer to measure growth.

Three tubes, without added oil, were included as controls at the lowest sediment dilution for each sample. Control tubes consistently exhibited either negligible or no growth. Therefore, growth in tubes containing oil was considered to be a result of hydrocarbon utilization, and not due to the addition of nutrients in the sediment inoculum.

The percentage of hydrocarbon-utilizing bacteria was determined for each sample by dividing the number of hydrocarbon utilizers per ml wet sediment by the number of viable heterotrophic bacteria per ml wet sediment and multiplying by 100.

Analysis of variance was performed on $\log_e$ transformed data to detect significant differences in the spatial and seasonal distribution of hydrocarbon-utilizing bacteria. Linear regression analysis was used to determine the relationship between hydrocarbon utilizers and field sampling variables. Analysis of variance and linear regression analysis followed standard formulas and procedures (Steel and Torrie 1960). A probability level of 0.05 was set to establish a significant difference in these tests.

## RESULTS

Station depths ranged from 1 m in Galveston Bay to 134 m on the south Texas outer continental shelf (Table 1). South Texas sediment exhibited less seasonal variation in temperature than did shallower nearshore and estuarine sediment. Sediment temperature was highest in summer and lowest in winter at all four sites. Station salinities were highest and fluctuated least at south Texas stations. Salinities were lowest and most variable at estuarine stations. Statistical analysis of the spatial distribution of total viable heterotrophic bacteria indicated that average populations over

TABLE 1

Range of values for field variables monitored at sampling sites.

| Site | | Station depth (m) | Sediment temp (°C) | Water salinity (°/oo) | Total viable heterotrophic bacteria per ml wet sediment x $10^4$ |
|---|---|---|---|---|---|
| South Texas | ( 72)[1] | 18-134 | 17-27 | 28-37 | 4.6 - 130 |
| West Hackberry | (156) | 7-13 | 9-28 | 16-28 | 12.0 - 6400 |
| Weeks Island | (156) | 6-13 | 10-30 | 13-32 | 0.2 - 1500 |
| Galveston Bay | ( 64) | 1-3 | 4-31 | 0-28 | 2.7 - 9100 |
| Total | 448 | | | | |

[1]Number of sediment samples analyzed.

the year were highest in Galveston Bay sediment and lowest in south Texas sediment. Along south Texas transects perpendicular to the shore, total viable heterotrophic bacteria decreased seaward from $7.9 \times 10^5$ to $2.2 \times 10^5$ per ml wet sediment.

Hydrocarbon-utilizing bacteria were detected in 438 of 448 sediment samples analyzed. Population densities ranged from $8.0 \times 10^1$ to $1.1 \times 10^6$ per ml wet sediment. On an average basis over the year, numbers of hydrocarbon utilizers were highest in Galveston Bay sediment and lowest in south Texas sediment (Table 2). Along south Texas transects perpendicular to the shore, hydrocarbon-utilizing bacteria decreased seaward from $17.3 \times 10^5$ to $2.6 \times 10^5$ per ml wet sediment. Significant seasonal differences were recorded at all four sites, but highest densities occurred during summer or fall (Table 2). Seasonal fluctuations in population levels were significantly

TABLE 2

Spatial and seasonal distribution of hydrocarbon-utilizing bacteria of sediment. Values represent mean ± 1 SD hydrocarbon utilizers per ml wet sediment x $10^5$.

| Season | South Texas[2] | West Hackberry[2] | Weeks Island[2] | Galveston Bay[2] |
|---|---|---|---|---|
| Summer | | 61.6 ± 89.2 (28) | 172.0 ± 295.0 (28) | 107.0 ± 136.0 (29) |
| Fall | 23.5 ± 35.8 (25)[3] | 82.8 ± 80.6 (26) | 75.8 ± 103.0 (23) | 515.5 ± 433.6 (21) |
| Winter | 4.7 ± 9.7 (18) | 24.6 ± 43.9 (10) | 13.5 ± 26.1 (12) | 1.1 ± 2.4 ( 6) |
| Spring | 3.1 ± 5.1 (21) | 46.8 ± 36.9 (22) | 64.5 ± 190.0 (22) | 198.0 ± 280.0 (26) |
| Annual[1] | 10.4 ± 23.3 | 53.9 ± 69.3 | 81.6 ± 190.0 | 209.0 ± 323.0 |

[1]Significant difference between sites at $P < 0.05$.
[2]Significant difference between seasons at $P < 0.05$.
[3]Mean sediment temperature (°C).

correlated with sediment temperature at all sites except Galveston Bay.

The percentage of hydrocarbon-utilizing bacteria ranged from 0.04 to 46.0%. Seventy percent of the sediment samples contained less than 2% hydrocarbon utilizers. On an average basis over the year, the percentage of hydrocarbon utilizers was highest in Weeks Island sediment. Significant seasonal differences were recorded at all four sites, with the highest percentages during fall or winter.

## DISCUSSION

Hydrocarbon-utilizing bacteria were detected in 438 of 448 sediment samples collected from four diverse and geographically distinct sites in the northwestern Gulf of Mexico. These results suggest that hydrocarbon utilizers and the potential for oil biodegradation are widespread in sediment from this region. However, the effectiveness of hydrocarbon utilizers in oil removal will depend on environmental factors such as oxygen, temperature, salinity, turbulence, organic matter, and nutrients (Zobell 1969, 1973).

Hydrocarbon-utilizing bacteria, although widespread, are not evenly distributed. Analysis of spatial variations indicated that populations were highest in estuarine sediment and lowest in offshore sediment. On the south Texas outer continental shelf, hydrocarbon utilizers decreased seaward along transects perpendicular to the shore. These findings suggest a trend for the spatial distribution of hydrocarbon-utilizing bacteria in the Gulf of Mexico, with greatest concentrations in estuarine sediment and with decreasing concentrations with increasing distance from shore. Several previous studies in other ocean regions have also reported greatest numbers of hydrocarbon utilizers near land (Gunkel 1973; Mulkins-Phillips and Stewart 1974). The spatial distribution of hydrocarbon utilizers in this and other ocean regions may be attributed to chronic hydrocarbon input nearshore (Zobell 1969).

The number of hydrocarbon-utilizing bacteria exhibited significant seasonal fluctuations at all four sites. The highest numbers were in the summer or fall. Temporal changes in population levels clearly indicate that hydrocarbon utilizers from the Gulf of Mexico respond to seasonal fluctuations in environmental parameters. Temperature may be especially important in controlling the seasonal abundance of hydrocarbon utilizers. Temperature was significantly correlated with number of hydrocarbon utilizers at all sites except Galveston Bay. The lack of correlation in Galveston Bay may be largely due to rapid fluctuations in temperature which occur in this shallow-water environment.

Several final points of discussion relate to the method and medium used to enumerate hydrocarbon-utilizing bacteria. Hydrocarbon utilizers were enumerated in the present study using the MPN method in which positive tubes were determined by visual inspection. A recent modification of the MPN method using $^{14}$C-hexadecane-spiked crude oil has been developed in which positive tubes are determined by assay of $^{14}CO_2$ (Atlas 1979). Although this radioisotope technique is undoubtedly more sensitive than the method used in the present study, it may have limited application in large-scale surveys because the method is tedious, requires expensive equipment, and necessitates familiarity with radioisotope methodology.

The basal-oil medium used to enumerate hydrocarbon-utilizing bacteria in the present study had a salinity of 30‰. This salinity may have selected for only a portion of the population. Hydrocarbon-utilizing bacteria with a salinity preference lower than 30‰ may not have been able to grow in the medium employed.

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## LITERATURE CITED

ATLAS, R. M. 1979. Measurement of hydrocarbon biodegradation potentials and enumeration of hydrocarbon-utilizing microorganisms using carbon-14 hydrocarbon-spiked crude oil, p. 196–204. In J. W. Costerton and R. R. Colwell (ed.) *Native Aquatic Bacteria: Enumeration, Activity and Ecology.* ASTM STP 695, Philadelphia.

_____ and R. BARTHA. 1973. Abundance, distribution and oil biodegradation potential of microorganisms in Raritan Bay. *Environmental Pollution.* 4:291–300.

BROWN, L. R., M. LIGHT, and C. D. MINCHEW. 1980. Geographic distribution of petroleum hydrocarbons in surficial bottom sediments of the Gulf of Mexico, p. 181–205. In R. A. Geyer (ed.) *Marine Environmental Pollution.* Volume I. *Hydrocarbons.* Elsevier Scientific Publ. Co., Amsterdam.

COLWELL, R. R. 1979. Enumeration of specific populations by the most-probable-number (MPN) method, p. 56-61. In J. W. Costerton and R. R. Colwell (ed.) *Native Aquatic Bacteria: Enumeration, Activity, and Ecology.* ASTM STP 695, Philadelphia.

CROW, S. A., M. A. HOOD and S. P. MEYERS. 1975. Microbiological aspects of oil intrusion in southeastern Louisiana, p. 221–227. In A. W. Bourquin, D. G. Ahearn, and S. P. Meyers (ed.) *Impact of the Use of Microorganisms on the Aquatic Environment.* Environmental Protection Agency, Washington, D.C.

FLOODGATE, G. D. 1972. Biodegradation of hydrocarbons in the sea, p. 153–171. In R. Mitchell (ed.) *Water Pollution Microbiology.* Wiley-Interscience, N.Y.

GEYER, R. A. 1980. Introduction, p. 1–18. In R. A. Geyer (ed.) *Marine Environmental Pollution.* Volume I. *Hydrocarbons.* Elsevier Scientific Publ. Co., Amsterdam.

GUNKEL, W. 1973. Distribution and abundance of oil-oxidizing bacteria in the North Sea, p. 127–139. In D. G. Ahearn and S. P. Meyers (ed.) *The Microbial Degradation of Oil Pollutants.* Center for Wetland Resources Publ. No. LSU-SG-73-01, Baton Rouge.

HOOD, M. A., W. S. BISHOP, Jr., F. W. BISHOP, S. P. MEYERS and T. WHELAN III. 1975. Microbial indicators of oil-rich salt marsh sediments. *Applied Microbiology.* 30:982–987.

MULKINS-PHILLIPS, G. J. and J. E. STEWART. 1974. Distribution of hydrocarbon-utilizing bacteria in northwestern Atlantic waters and coastal sediments. *Canadian Journal of Microbiology.* 20:955–962.

OPPENHEIMER, C. H., S. SIEGEL, L. DAY and C. DUNCAN. 1980. Distribution of hydrocarbon-oxidizing bacteria on the Georgia shelf area and oil-degrading activities, p. 265–290. In R. A. Geyer (ed.) *Marine Environmental Pollution.* Volume I. *Hydrocarbons.* Elsevier Scientific Publ. Co., Amsterdam.

OUJESKY, H. V., O. W. Van AUKEN, J. ALLEN, W. BROOKS, A. KASTER, B. REED and C. WILSON. 1979. Water column bacteriology, p. 8–1 to 8–128. In Environmental Studies, South Texas Outer Continental Shelf, Biology and Chemistry. Volume I. Bureau of Land Management, Washington, D.C.

ROUBAL, G. and R. M. ATLAS. 1978. Distribution of hydrocarbon-utilizing microorganisms and hydrocarbon biodegradation potentials in Alaskan continental shelf areas. *Applied and Environmental Microbiology.* 35:897–905.

STEEL, R. G. D. and J. H. TORRIE. 1960. *Principles and procedures of statistics.* McGraw-Hill, N.Y. 481p.

WALKER, J. D. and R. R. COLWELL. 1973. Microbial ecology of petroleum utilization in Chesapeake Bay, p. 685–690. In API/EPA/USCG Conference on Prevention and Control of Oil Spills. American Petroleum Institute, Washington, D.C.

ZOBELL, C. E. 1969. Microbial modification of crude oil in the sea, p. 317–326. In Proceedings of the API/FWPCA Joint Conference on Prevention and Control of Oil Spills. American Petroleum Institute, Washington, D.C.

_____. 1973. Microbial degradation of oil: present status, problems, and perspectives, p. 3–16. In D. G. Ahearn and S. P. Meyers (ed.) *The Microbial Degradation of Oil Pollutants.* Center for Wetland Resources Publ. No. LSU-SG-73-01, Baton Rouge.

_____ and J. F. PROKOP. 1966. Microbial oxidation of mineral oils in Barataria Bay bottom deposits. *Zeitschrift für allegemeine Mikrobiologie.* 6:143–162.

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# NEW RECORDS AND RANGE EXTENSIONS OF DEEPWATER ALGAE FROM EAST FLOWER GARDEN BANK, NORTHWESTERN GULF OF MEXICO

N. J. Eiseman and S. M. Blair

*Harbor Branch Foundation, RR 1, Box 196, Fort Pierce, Florida 33450*

## ABSTRACT

Deepwater benthic algal collections were made by the research submersibles *Johnson-Sea-Link I* and *Diaphus* in the East Flower Garden Bank region of the Northwestern Gulf of Mexico during September of 1976, 1977, 1978, and 1980. Forty-one species were identified, 33 of which were new records for the Northwestern Gulf (Texas). Five species *Halimeda gracilis, Titanophora incrustans, Compsothamnion thuyoides, Apoglossum ruscifolium,* and *Searlesia subtropica,* are reported for the first time from the Gulf of Mexico.

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## INTRODUCTION

The offshore flora of the northwestern Gulf of Mexico is still poorly known. The west coast of Florida, the Florida Keys and the Yucatan peninsula are well investigated but few studies have been conducted in the northwestern region. The Gulf has been shown to support a multicomponent flora. There is a cool temperate flora during the winter in the northern portions (Humm and Caylor 1957, Humm and Darnell 1959, Conover 1964, Earle 1969), a subtropical and tropical assemblage in the southern portions (Taylor 1935, Humm 1952a, Huerta M. 1964, Huerta M. and Garza Barrientos 1966, Cheney 1976), and a ubiquitous flora seen throughout the Gulf (Conover 1964, Earle 1972). Earle (1972) has listed 580 species of Chlorophyta, Phaeophyta, and Rhodophyta for the Gulf and notes that large differences are seen in species numbers recorded from the different regions. At present, only 160 species have been recorded from Texas, Mississippi and Louisiana as compared to 340 for Mexico and Yucatan and 490 for the west coast of Florida and the Florida Keys. The discrepancy appears attributable to a combined effect of sampling intensity and the presence of the subtropical and tropical components in the southern areas. Humm and Taylor (1961) predicted that a tropical flora could be in the northern regions in the deeper offshore waters. This prediction was later supported by studies in the Northeastern Gulf (Earle 1969, Dawes and van Breedveld 1969, Cheney and Dyer 1974).

To date the studies dealing with offshore benthic algae of the northwestern Gulf of Mexico have been restricted to nearshore, shallow water habitats. The deep water collections reported here were taken by the Harbor Branch Foundation's submersible *Johnson-Sea-Link I* during September of 1980. These data have been supplemented by collections from the submersible *Diaphus* (Texas A & M University) during September of 1976, 1977 and 1978.

## METHODS

Collections were made on or near the East Flower Garden Bank (27°54′N, 93°35′W) approximately 175 kilometers SSE of Galveston, Texas. Samples taken by *Johnson-Sea-Link I* (JSLI) were collected either by a lockout diver or with a 10 x 10 cm grab sampler on the sub's manipulator arm. All *Diaphus* samples were collected by a manipulator. Specimens were preserved in 5% formalin in seawater. Representative specimens from the collections are on deposit in the Harbor Branch Foundation Herbarium (HBFH).

## RESULTS AND DISCUSSION

A total of 41 species was identified from the samples (15 Chlorophyta, 6 Phaeophyta, and 20 Rhodophyta; Table 1). The small number of species (cf. Dawes and van Breedveld, 1969) may be due to the effects of a large hurricane which passed over the area just prior to the major sampling. Five species, *Halimeda gracilis, Titanophora incrustans, Compsothamnion thuyoides, Apoglossum ruscifolium* and *Searlesia subtropica* are new records for the Gulf of Mexico. Thirty-three of the species collected (see Table 1) represent new records and range extensions for the northwestern Gulf.

Previous descriptions of the nearshore algae of Texas show the flora to be similar to that of Mississippi and Louisiana with a minor subtropical component (Baca *et al.* 1977, Table 1). However, few investigators have studied the deepwater component. Bright and Pequegnat (1974) mention seven genera from the Flower Garden Banks and Kapraun (1974) listed 10 species from the shallower waters (20-27 m) of that region. The presence of members of the Siphonocladales, Caulerpales, and Dictyotales in the present collections ally the offshore deepwater flora more closely with the subtropical and tropical portions of the Gulf than had been previously appreciated. These results support Humm and Taylor's (1961) postulation of a floral diversity gradient with depth, offshore in the northern Gulf.

## COLLECTIONS

Pertinent data (date, lat., long., and depth) are given below for each dive referenced in Table 1.

*Johnson-Sea-Link I* collections: JSLI-903; 10 September 1980; 27°54.5′N, 93°35.4′W; 68.8 m. JSLI-904; 10 September 1980; 27°54.54′N, 93°35.48′W; 55.8 m. JSLI-906; 11 September 1980; 27°54.54′N, 93°35.48′W; 53.3 m. JSLI-910; 12 September 1980; 27°54.5′N, 93°35.4′W; 68.6 m.

TABLE 1

Collection dives and previous reports of species collected.

| | Dive | South and S.W. Gulf | Texas | Mississippi & Louisiana | Florida |
|---|---|---|---|---|---|
| Chlorophyta | | | | | |
| *Anadyomene stellata* (Wulfen) C. Agardh | (D) 78-G9D7 | 8,27,28 | 8 | 8 | 4,5,6,8,10,15,19,24,27 |
| *Caulerpa microphysa* (Weber-van Bosse) J. Feldman | JSLI-906; (D) 78-G9D7 | 8,11 | | | 2,4,5,6,8,27 |
| *C. peltata* Lamouroux | JSLI-903; (D) 78-G9D7 | 8,13,27 | | | 2,5,6,8,19,25,27 |
| *C. racemosa* Forsskål (J. Agardh) | (D) 77-G-10-2 | | | | |
| *V. macrophysa* (Kützing) Taylor | | 8*,11,27*,28* | | | 4*,6*,8*,27 |
| *Codium taylori* Silva | (D) 78-G9D7 | 8,18,27 | | | 8,19,24,25,27 |
| *Halimeda discoidea* Decaisne | (D) 78-G9III#125 | 8,12 | | | 2,4,5,6,8,19,25,27 |
| *H. gracilis* Harvey | JSLI-906; (D) 78-9GD5 | | | | |
| *Microdictyon boergesenii* Setchell | JSLI-906 | | | 8 | 4,8,27 |
| Unknown Palmellaceae | JSLI-903; (D) 78-9GIII | | | | |
| *Struvea* sp. (fragment) | JSLI-903 | | | | |
| *Udotea cyanthiformis* Decaisne | (D) 78-G9D7 | 8 | | | 6,8,27 |
| *U. flabellum* (Ellis & Solander) Lamouroux | JSLI-906; (D) 78-9GD7 | 8,12,28 | | | 2,4,5,6,8,19,25,27 |
| *Ulva lactuca* Linnaeus† | JSLI-910 | 8,18,19,27 | 3,8,9,18,19,22,27 | 8,16,19,20,23,27 | 8,10,14,15,19,24,27 |
| *Valonia macrophysa* Kützing | (D) 78-G9D7 | | | 2,4,8,25,27 | |
| *V. ventricosa* J. Agardh | JSLI-906; JSLI-910 | 8,11,18,27,28 | | | 4,5,8,27 |
| Phaeophyta | | | | | |
| *Dictyopteris justii* Lamouroux | JSLI-903 | 8,13,27,28 | | | 6,7,8,27 |
| *Dictyota bartayresii* Lamouroux | JSLI-904 | 8,11,18,27 | | 20 | 2,4,5,7,8,15,27 |
| *D. dichotoma* (Hudson) Lamouroux | JSLI-904; JSLI-906 | 8,18,27,28 | 3,8,9,18,21,22 | 8,16,17,20,23 | 2,4,5,6,7,8,10,24,25,27 |
| *Lobophora variegata* (Lamouroux) Womersly | JSLI-904; JSLI-906 (D) 78-G9D7 | 8,28 | | 20 | 4,5,6,7,8 |
| *Spatoglossum schroederi* (Mertens) Kützing | JSLI-903 | 8,18,27 | 1 | | 4,6,7,8,25,27 |
| *Stypopodium zonale* (Lamouroux) Papenfuss | JSLI-906; JSLI-910 (D) 78-G9D7 | 8,28 | | | 7,8,27 |

* Variety not designated.

† Attributable to this species described for the tropics. However Kapraun (personal communication) suggests that this species does not occur in the New World.

TABLE 1 (Continued)

| | Dive | South and S.W. Gulf | Texas | Mississippi & Louisiana | Florida |
|---|---|---|---|---|---|
| Rhodophyta | | | | | |
| *Amphiroa rigida* Lamouroux *V. antillana* Børgesen | JSLI-903; JSLI-904 | 8,11,18 | | | 4,6,8,25,27 |
| *A. tribulus* (Ellis and Solander ) Lamouroux | (D) 78-G9D7 | 8,27 | | | 8,27 |
| *Apoglossum ruscifolium* (Turner) J. Agardh | JSLI-903 | | | | |
| *Botryocladia occidentalis* (Børgesen) Kylin | JSLI-906 | | | | 2,4,5,6,8,25,27 |
| *Chrysymenia halymenioides* Harvey | (D) 78-GIII | | | | 2,6,8,27 |
| *Coelarthrum albertisii* (Piccone) Børgesen | (D) 78-9GD7#126; (D) 76-G8-III 76-35 | | | | 2,6 |
| *Compsothamnion thuyoides* (Smith) Schmitz | JSLI-903; JSLI-904 | | | | |
| *Cryptonemia* sp. | (D) 78-G9III#120 | | | | |
| *Dasya corymbifera* J. Agardh | JSLI-903 | | | | 4,6,8,15 |
| *Fauchea hassleri* Howe & Taylor | (D) 78-G9III#126 | | | | 2,8 |
| *Galaxaura cylindrica* (Ellis and Solander) Lamouroux | (D) 78-G-10-2 | 8 | | | 4,8,27 |
| *G. oblongata* (Ellis and Solander) Lamouroux | JSLI-906 | 8,11 | | | 8,27 |
| *Grateloupia filicina* (Wulfen) C. Agardh | JSLI-904 | 8,11,12,18 | 3,8,9,21 | 8,16 | 2,8,24,27 |
| *Hypoglossum teniufolium* (Harvey) J. Agardh | JSLI-904 | | | | 2,4,5,6,8,15,25,27 |
| *Kallymenia westii* Ganesan | (D) 78-G9III#126 | | | | 2,8,27 |
| *Peyssonnelia rubra* (Greville) J. Agardh | JSLI-904; (D) 78-G-10-2 | | | | 2,4,5,6,8,25,27 |
| *P. simulans* Weber-van Bosse | JSLI-903; JSLI-904 | | | | 4,8 |
| *Pterocladia barteletii* Taylor | (D) 78-G9D7 | | 8,9,27 | | |
| *Searlesia subtropica* (Schneider) Schneider & Eiseman | JSLI-903 | | | | 26 (East Coast) |
| *Titanophora incrustans* (J. Agardh) Børgesen | JSLI-903; JSLI-904; JSLI-910 | | | | 8 (East Coast) |

1. Baca *et al.* 1977
2. Cheney and Dyer 1974.
3. Conover 1964.
4. Croley and Dawes 1970.
5. Dawes *et al.* 1967
6. Dawes and van Breedveld 1969.
7. Earle 1969.
8. Earle 1972.
9. Edwards and Kapraun 1973.
10. Hamm and Humm 1976.
11. Huerta M. 1964.
12. Huerta M. and Garza Barrientos 1966.
13. Humm 1952a.
14. Humm 1952b.
15. Humm 1964.
16. Humm and Caylor 1957.
17. Humm and Darnell 1959.
18. Humm and Hildebrand 1962.
19. Humm and Taylor 1961.
20. Kapraun 1974.
21. Kapraun 1980.
22. Lowe and Cox 1978.
23. Mullahy 1959.
24. Phillips 1960.
25. Phillips and Springer 1960.
26. Schneider and Eiseman 1979.
27. Taylor 1960.
28. Taylor 1972.

*Diaphus* collections: (D) 76-G8III 76-35; 25 September 1976; 27°54′32″N, 93°35′49″W; 71.5 m. (D) 77-G-10-2; 24 September 1977; 27°53′N, 93°18′W; 55-64 m. (D) 78-G9III#6; 1 September 1978; 27°54′32″N, 93°35′49″W; 91 m. (D) 78-G9III#120; 17 September 1978; 27°54′56″N, 92°22′15″W; 60-80 m. (D) 78-G9III#126; 20 September 1978; 27°49′15″N, 92°53′36″W; 95-105 m. (D) 78-G9D5; 30 September 1978; 27°54′32″N, 93°35′49″W; 48.7 m. (D) 78-G9D7; 2 September 1978; 27°54′32″N, 93°35′49″W; 58 m.

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## LITERATURE CITED

BACA, B. J., E. R. COX and L. O. SORENSEN. 1977. Observations on several benthic marine algae from South Padre Island, Texas, U.S.A. *Southwestern Naturalist.* **21**:459–462.

BRIGHT, T. J. and L. H. PEQUEGNAT (Ed.). 1974. *Biota of the West Flower Garden Bank.* Gulf Publishing Co., Houston, Texas. 435 pp.

CHENEY, D. P. 1976. Spatial and seasonal distribution and floristic affinities of the benthic algae of the Gulf of Mexico. *Journal of Phycology.* **12** (suppl.): 28–29.

_____ and J. P. DYER III 1974. Deep-water benthic algae of the Florida Middle Grounds. *Marine Biology.* **27**:185–190.

CONOVER, J. T. 1964. The ecology, seasonal periodicity and distribution of benthic plants in some Texas lagoons. *Botanica Marina.* **7**:4–41.

CROLEY, F. C. and C. J. Dawes. 1970. Ecology of the algae of a Florida Key, Part 1: a preliminary checklist, zonation and seasonality. *Bulletin of Marine Science.* **20**:165–185.

DAWES, C. J., S. A. EARLE and F. C. CROLEY. 1967. The offshore benthic flora of the southwest coast of Florida. *Bulletin of Marine Science.* **17**:211–231.

_____ and J. F. van BREEDVELD. 1969. *Memoirs of the Hourglass Cruises.* Vol. 1, part II. Marine Research Laboratory, Department of Natural Resources, St. Petersburg, Florida. 47 pp.

EARLE, S. A. 1969. Phaeophyta of the eastern Gulf of Mexico. *Phycologia.* **7**:71–254.

_____. 1972. Benthic Algae and Seagrasses. pp. 15–18, Appendix III. In El-Sayed *et al. Chemistry, primary productivity, and benthic algae of the Gulf of Mexico. Folio 22. The serial atlas of the marine environment.* American Geographical Society. New York, New York.

EDWARDS, P. and D. F. KAPRAUN. 1973. Benthic marine algal ecology in the Port Aransas, Texas area. *Contributions in Marine Science.* **17**:15–52.

HAMM, D. and H. J. HUMM. 1976. Benthic algae of the Anclote Estuary II. Bottom-dwelling species. *Quarterly Journal of Florida Academy of Science.* **39**:209–230.

HUERTA M., L. 1964. Algas marinas de la Barra de Tuxpan y de los arrecifes Blanquilla y Lobos. *Anales de la Escuela Nacional de Ciencias Biologicas.* **13**:5–21.

_____ and M. A. Barrientos Garza. 1966. Algas Marinas del littoral del Estado de Campeche. *Ciencia, Mexico.* **24**:193–200.

HUMM, H. J. 1952a. Marine algae of Campeche Banks. *Florida State University Studies.* No. (7).27.

_____. 1952b. Notes on the marine algae of Florida. I. The intertidal rocks at Marineland. *Florida State University Studies.* No. **7**:17–23.

_____. 1964. Epiphytes of the seagrass *Thalassia testudinum. Bulletin of Marine Science of the Gulf and Caribbean.* **14**:306–341.

_____ and R. L. CAYLOR. 1957. The summer marine flora of Mississippi Sound. *Publications of the Institute of Marine Science, University of Texas.* **4**(2):228–264.

_____ and R. M. DARNELL. 1959. A collection of marine algae from the Chandler Islands. *Publications of the Institute of Marine Science, University of Texas.* **6**:265–276.

———— and H. H. HILDEBRAND. 1962. Marine algae from the Gulf coast of Texas and Mexico. *Publications of the Institute of Marine Science, University of Texas.* **8**:227–268.

———— and S. E. TAYLOR. 1961. Marine Chlorophyta of the upper west coast of Florida. *Bulletin of Marine Science of the Gulf and Caribbean.* **11**:321–380.

KAPRAUN, D. F. 1974. Seasonal periodicity and spatial distribution of benthic marine algae in Louisiana. *Contributions in Marine Science.* **18**:139–167.

————. 1980. Summer aspect of algal zonation on a Texas USA jetty in relation to wave exposure. *Contributions in Marine Science.* **23**:101–110.

LOWE, G. C. and E. R. COX. 1978. Species composition and seasonal periodicity of the marine benthic algae of Galveston Island, Texas. *Contributions in Marine Science.* **21**:9–24.

MULLAHY, J. H. 1959. Preliminary survey of the algal flora of the Chandler Islands. *Proceedings of the Louisiana Academy of Sciences.* **22**:62–68.

PHILLIPS, R. C. 1960. Ecology and distribution of marine algae found in Tampa Bay, Boca Ciega Bay and at Tarpon Springs, Florida. *Quarterly Journal. Florida Academy of Sciences.* **23**:222–260.

———— and V. G. SPRINGER. 1960. Observations on the offshore benthic flora in the Gulf of Mexico off Pinellas County, Florida. *American Midland Naturalist.* **62**:362–381.

SCHNEIDER, C. W. and N. J. EISEMAN. 1979. *Searlesia,* a new genus from the western Atlantic based on *Membranoptera subtropica* (Rhodophyta, Delesseriaceae). *Phycologica.* **18**:319–324.

TAYLOR, W. R. 1935. Marine algae from the Yucatan Peninsula. *Publications. Carnegie Institution of Washington.* No. **461**:115–124.

————. 1960. *Marine algae of the Eastern Tropical and Subtropical Coasts of the Americas.* Univ. Michigan Press, Ann Arbor, Michigan. 870 pp.

————. 1972. Marine algae of the Smithsonian-Bredin expedition to Yucatan–1960. *Bulletin of Marine Science.* **22**:34–44.

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# LABORATORY STUDIES OF A MARINE COPEPOD (*TEMORA TURBINATA* DANA) TRACKING DINOFLAGELLATE MIGRATIONS IN A MINIATURE WATER COLUMN[1]

Jerry L. Bird[2] and Christopher L. Kitting

*The University of Texas, Marine Science Institute*
*Port Aransas Marine Laboratory, Port Aransas, Texas 78373*

## ABSTRACT

Dual water columns were used to examine the response of *Temora turbinata* to dinoflagellate migrations over 48-hour periods. *T. turbinata* migration was most pronounced in the presence of high concentrations of *Prorocentrum micans.* In the morning these copepods migrated to the surface parallel to the migration of *P. micans.* During the afternoon the animals drifted downward slightly; this descent accelerated at night. At lower concentrations of *P. micans, T. turbinata* exhibited a more complex migration pattern.

In the presence of *Cachonina niei,* which increased in concentration with depth, *T. turbinata* remained deeper in the water column than it did with *P. micans.* In the absence of food, *T. turbinata* soon descended to the bottom and remained there.

Although the method by which herbivores detect localized concentrations of phytoplankton remains to be determined, results of this study suggest that the behavior of *T. turbinata* may be modified in the presence of different types, distributions, and concentrations of food organisms. This ability for behavioral modification is clearly important to the herbivore in environments where food resources vary spatially and temporally.

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## INTRODUCTION

Distributional heterogeneity in planktonic communities is often attributed to both physical and biological factors. Variation in vertical distributions of zooplankton may result from diel vertical migration, which is usually characterized by nighttime residence in the upper regions of the water column and daytime residence deeper in the water column. The selective advantage of this behavior is believed to involve either predation pressure or resource utilization (McLaren 1963, 1974; Narver 1970; Zaret and Suffern 1976; Enright 1977).

[1] The University of Texas Marine Science Institute Contribution No. 544
[2] Present Address: Naval Ocean Research and Development Activities, Code 344, NSTL Station, Mississippi 39529, U.S.A.

Zooplankton may experience local food scarcity due to phytoplankton migration (Kamykowski 1976) or zooplankton overgrazing (Raymont 1980). In such cases, zooplankton would seek other resources. In order to investigate this possibility we studied the interactions between phytoplankton migration and *T. turbinata,* a copepod common on the Texas continental shelf (Fleminger 1956). *T. turbinata* displayed irregular migratory behavior in the field in 1978 (Bird 1981).

Miniature water columns were used to investigate these interactions because they facilitate greater environmental control, direct observation, and rapid experimental setup (Booker *et al.* 1976, Heaney and Eppley 1980, Kamykowski 1981). The major disadvantage of the miniature tank is that its small size may alter the natural behavior of migratory zooplankton. However, miniature tanks provide the opportunity to study short-term behavior of animals that migrate in response to phytoplankton movements.

## METHODS

Two Plexiglas® cylinders, 20.3 cm in diameter and 135 cm in length, were used to monitor the movements of the calanoid copepod, *Temora turbinata* and of its dinoflagellate prey, either *Prorocentrum micans* Ehrenberg or *Cachonina niei* Loeblich. Stock cultures of *T. turbinata* have been successfully maintained in our laboratory on unialgal diets of both phytoplankton species. The cylinders were housed in a walk-in environmental chamber. Overhead fluorescent lighting and temperature of the chamber were controlled on a 12:12 h cycle. Table 1 summarizes experimental variables of each experiment.

Filtered sea water (0.20–0.45 μm) for each experiment was enriched with nutrients to produce a GPM/10 or GPM/8 medium (Loeblich 1975). This medium stood undisturbed in the water columns for 24 h to equilibrate with room temperature and for turbulence to subside. The dinoflagellate was then introduced and allowed to adjust to the light and temperature regime for 12–24 h before addition of the copepods. Stock cultures of phytoplankton were incubated at 20°C in GPM medium (28‰). *P. micans* (UTEX LB 1003) and *C. niei* (UTEX LB 1564) cultures were obtained from the culture collection at The University of Texas at Austin.

*T. turbinata* was collected from the Aransas Pass Ship Channel. Within two hours of collection, copepods were sorted under a dissecting microscope by using a large-bore pipette with gentle suction and then introduced to the surface of the water columns. Depending on the experiment, 20 or 42 adults, or 84 late copepodites (CIV, CV) were used in each column.

The profiling regime consisted of determining water column temperature, *in vivo* fluorescence, and copepod distribution. Sampling was delayed 12 h after introduction of the copepods to minimize the effects of the handling and enable the copepods to locate their prey. Profiles were repeated at 3-h intervals for 24 to 48 h. Water column temperature was obtained with a thermistor attached to the chlorophyll profiling hose. This hose consisted of paired Tygon® tubes weighted by a glass vial containing lead. A peristaltic pump circulated water from the column to the fluorometer and back. *In vivo* fluorescence was measured by a Turner Designs Model 10 fluorometer, equipped with a 2-ml sample chamber, and recorded on a WeatherMeasure chart recorder. Residence time in the profiling system was 20 seconds. The hose intake was 5 cm above the exit. The profiling hose was pulled through the water at a rate of 1 cm/sec; therefore a small sample (0.2% of the total volume) was displaced upwards 15 cm during each profile. After each continuous fluorescence profile, calibration samples (34 ml) were obtained at 5 depths (5, 35, 65, 95, and 125 cm) for *in vitro* measurement of chlorophyll *a* with a Turner Model 111 fluorometer (Strickland and Parsons 1968).

Copepod distributions were observed visually. The copepods were easily visible in the water column. Copepods in 5-cm depth intervals were counted, and these data were combined into 15-cm intervals. Counting at night was aided by scanning with a narrow beam flashlight (2.4 cm

TABLE 1

**Water column experimental parameters.**

| Experiment No. | Subject[1] | No. | Food[2] Type | Medium | Salinity 0/00 | Temperature °C Day Surface | Day Bottom | Night Surface | Night Bottom |
|---|---|---|---|---|---|---|---|---|---|
| 1A | Adults | 20 | *P.m.* | GPM/10 | 28 | 19.14±1.02 | 17.85±0.59 | 17.67±0.33 | 17.53±0.23 |
| 1B | Adults | 20 | ... | GPM/10 | 28 | | | | |
| 2A | Adults | 42 | *P.m.* | GPM/8 | 28 | 19.45±0.65 | 17.39±0.44 | 17.89±0.56 | 17.34±0.28 |
| 2B | Copepodites | 84 | *P.m.* | GPM/8 | 28 | | | | |
| 3A | Adults | 42 | *C.n.* | GPM/8 | 25 | 24.25±0.29 | 23.40±0.12 | 23.55±0.53 | 23.15±0.26 |
| 3B | Copepodites | 84 | *C.n.* | GPM/8 | 25 | | | | |
| 4A | Adults | 42 | *P.m.* | GPM/8 | 25 | 24.09±0.32 | 23.45±0.23 | 23.45±0.23 | 23.16±0.26 |
| 4B | Copepodites | 84 | *P.m.*[3] | GPM/8 | 25 | | | | |
| 5A | Adults | 42 | *P.m.* | GPM/8 | 24 | 25.16±1.03 | 24.30±0.69 | 23.21±0.72 | 22.93±0.57 |
| 5B | Copepodites | 82 | *P.m.* | GPM/8 | 24 | | | | |

[1] Adults = mixed male and female, Copepodites = late stages, mostly CIV and CV.
[2] *P.m.* = *Prorocentrum micans*, *C.n.* = *Cachonina niei*
[3] contains an unidentified diatom

diameter) with a red filter (Tiffin 25A, Red 1). The flashlight produced minimal effects on the copepods.

A small number of animals was undetected in some profiles in each experiment. This undetected fraction averaged 13.5% ± S.D. 8.1% of the total number introduced to the cylinder. These animals were thought to be on the bottom where accurate enumeration was difficult. Reflections on the Plexiglas caused mirror images and phytoplankton settled on the bottom in dense patches, which made detection difficult.

The Kolomogorov-Smirnov test was used to compare day and night distributions within each column and the distribution between the two columns. The K.-S. test utilizes cumulative frequencies, with 0% occurring at the surface, and thus ameliorates the previously mentioned sampling problems. The K.-S. statistic ($d_{max}$) estimates the maximum difference in the cumulative frequencies of two distributions (Siegel 1956).

## RESULTS

Adult *T. turbinata* were used in 5 experiments and copepodites in 4 experiments. Animal abundance at each depth was expressed as a percentage of the total number of animals introduced into the column. In the following figures, depths of the 20, 40, 60 and 80th percentiles (cumulative from the surface) were plotted for each profile to facilitate comparison of *T. turbinata* distributions.

**Experiment 1.** Adults without and with high concentrations of *P. micans.*

Figure 1 shows distributions of *P. micans* and Figure 2 shows the distributions of *T. turbinata* without (a) and with (b) *P. micans.*

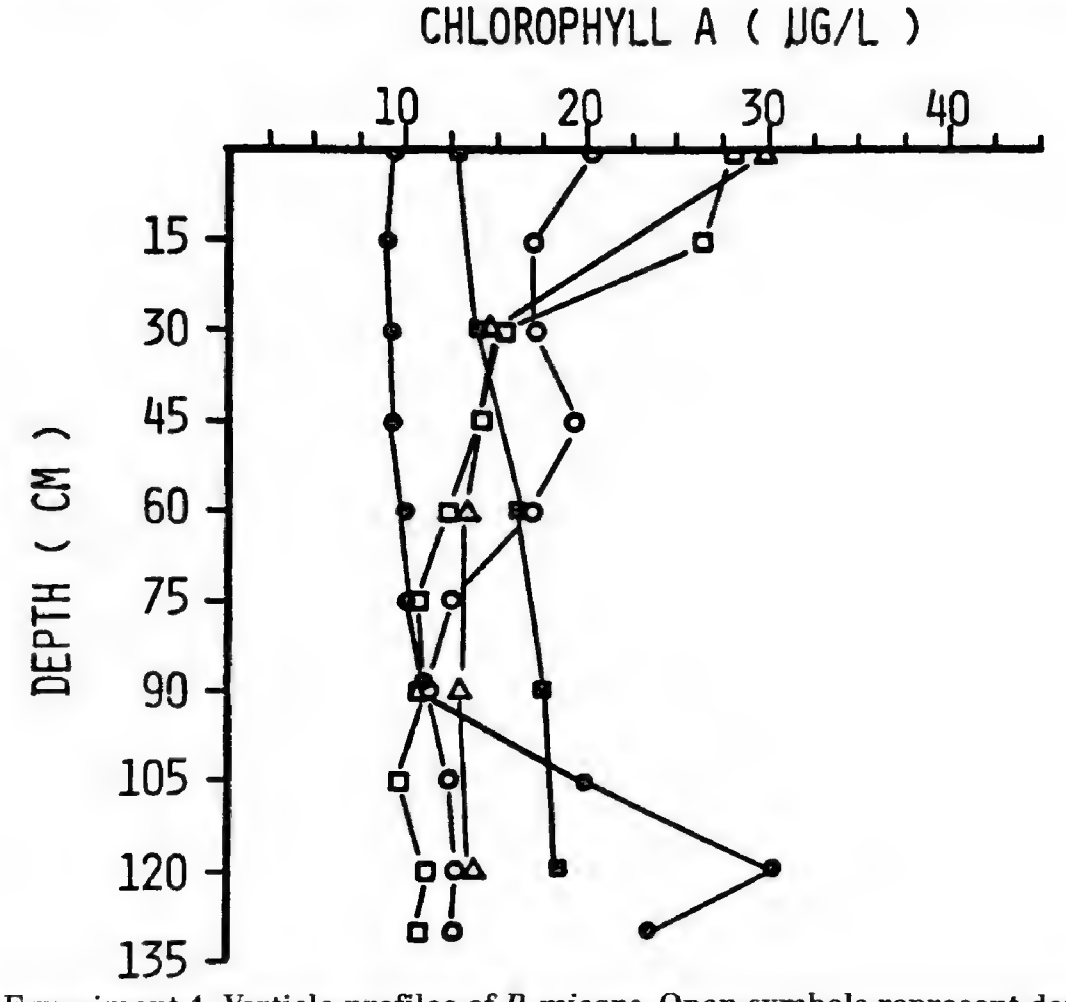


FIG. 1. Experiment 1. Verticle profiles of *P. micans.* Open symbols represent daytime values and closed symbols represent nighttime values for day 1 (circles), day 2 (squares), and day 3 (triangles). See Fig. 2 for light–dark cycle.

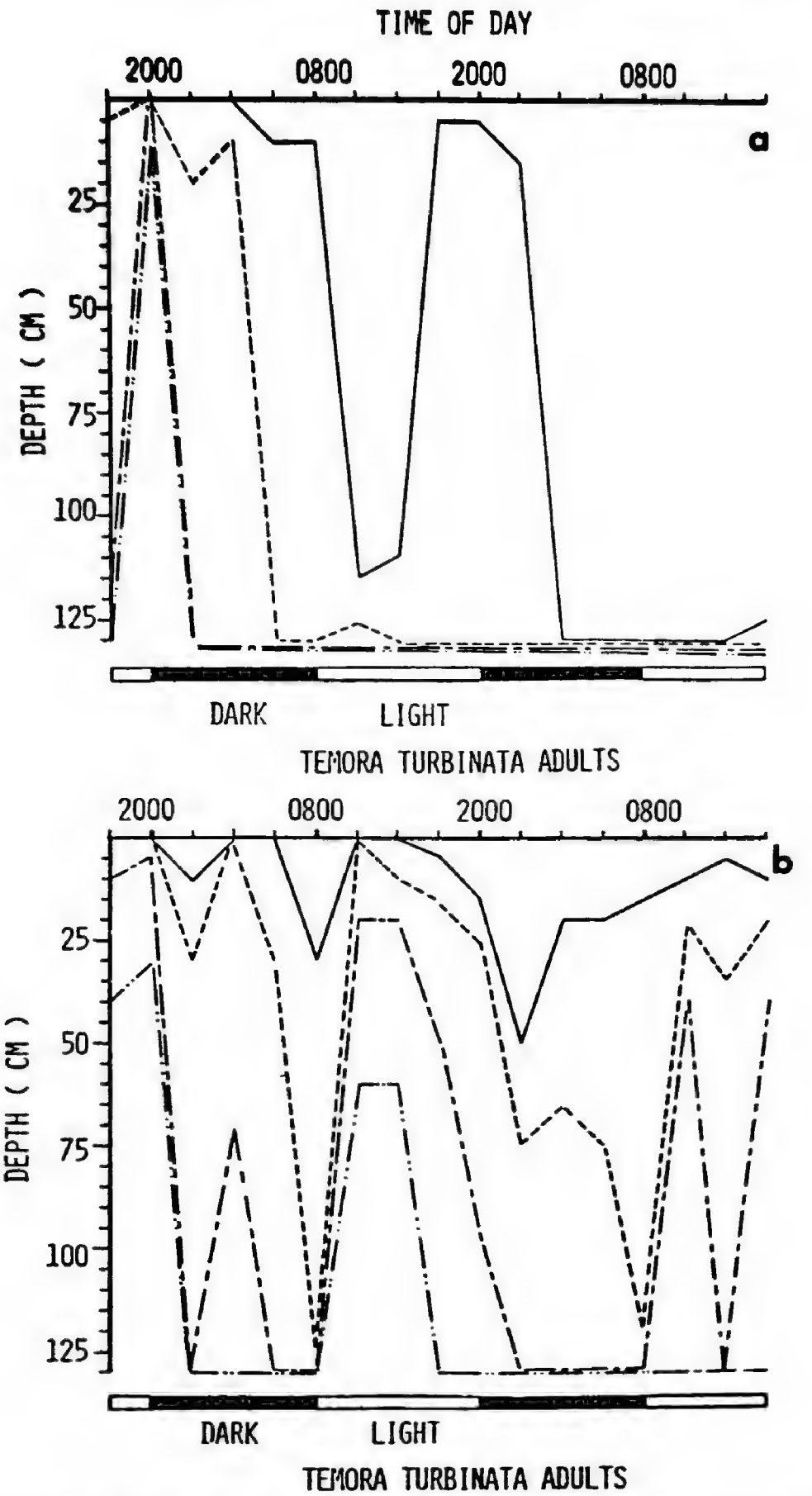


FIG. 2. Vertical distributions of *T. turbinata* in experiment 1(a) in the absence of *P. micans* and (b) in the presence of *P. micans*. Depths of the 20th (_____), 40th (- - -), 60th (__ - __), and 80th (__. .__), percentile are shown. The light and dark horizontal bar represents the light cycle.

Initial distributions of *T. turbinata* in the two columns were similar, but in the absence of *P. micans* (Fig. 2a), most animals remained on the bottom throughout the rest of the experiment. In the column without food migrating

individuals ascended and descended later than in the column with food, and day and night distributions were not significantly different from each other.

In the column with *P. micans*, the dinoflagellate concentrated near the surface during the day and near the bottom during the night. *T. turbinata* migrated in phase with *P. micans*. *T. turbinata* day and night distributions differed significantly (Kolomogorov-Smirnov 2-sample test, $P < 0.02$). The most prominent feature of the *T. turbinata* migration pattern was a morning rise of the population. Late in the day there was a downward movement, which accelerated at night. *T. turbinata* daytime distributions in the presence of food were different from *T. turbinata* daytime distributions in the absence of food ($P < 0.01$) but nighttime distributions in the presence and absence of food did not differ significantly.

**Experiment 2.** Adults and copepodites with high concentrations of *P. micans*.

*P. micans* concentrations and gradients were highest during this experiment. *P. micans* distributions became more homogeneous at night (Fig. 3a,b) unlike the downward migration at night in the previous experiment.

Adult *T. turbinata* exhibited their simplest migration pattern in this experiment (Fig. 4a). Adults were near the surface during the day and commenced their descent prior to darkness. Upward migration occurred between 0800 and 1100. Distributional differences between the two nights was due to a less pronounced descent the second night. Adult *T. turbinata* day and night distributions were significantly different ($P < 0.01$).

Copepodites (Fig. 4b) behaved like the adults but remained slightly deeper. Copepodite day and night distributions were significantly different from each other ($P < 0.01$). Due to the deeper position of the copepodites, adult and copepodite distributions were significantly different during the day ($P < 0.01$).

**Experiment 3.** Adults and copepodites with the dinoflagellate *Cachonina niei*.

The dinoflagellate *C. niei* (Fig. 5a,b) was poorly migratory at the salinity used in the experiment (25‰) (Kamykowski 1981); it concentrated near the bottom. *T. turbinata* adults and copepodites were distributed (Fig. 6a,b) differently from the previous experiments. Both adults and copepodites were deeper in the water column and descended during the day. With darkness, several adults and copepodites moved upward. There were no significant differences seen between day-night distributions within each column or population distributions between columns.

**Experiment 4.** Adults with low concentrations and copepodites with increasing concentrations of phytoplankton.

This experiment differed from the previous experiments in two respects. Concentrations of *P. micans* were lower, and an unidentified diatom was fortuitously introduced into the column with copepodites and reproduced

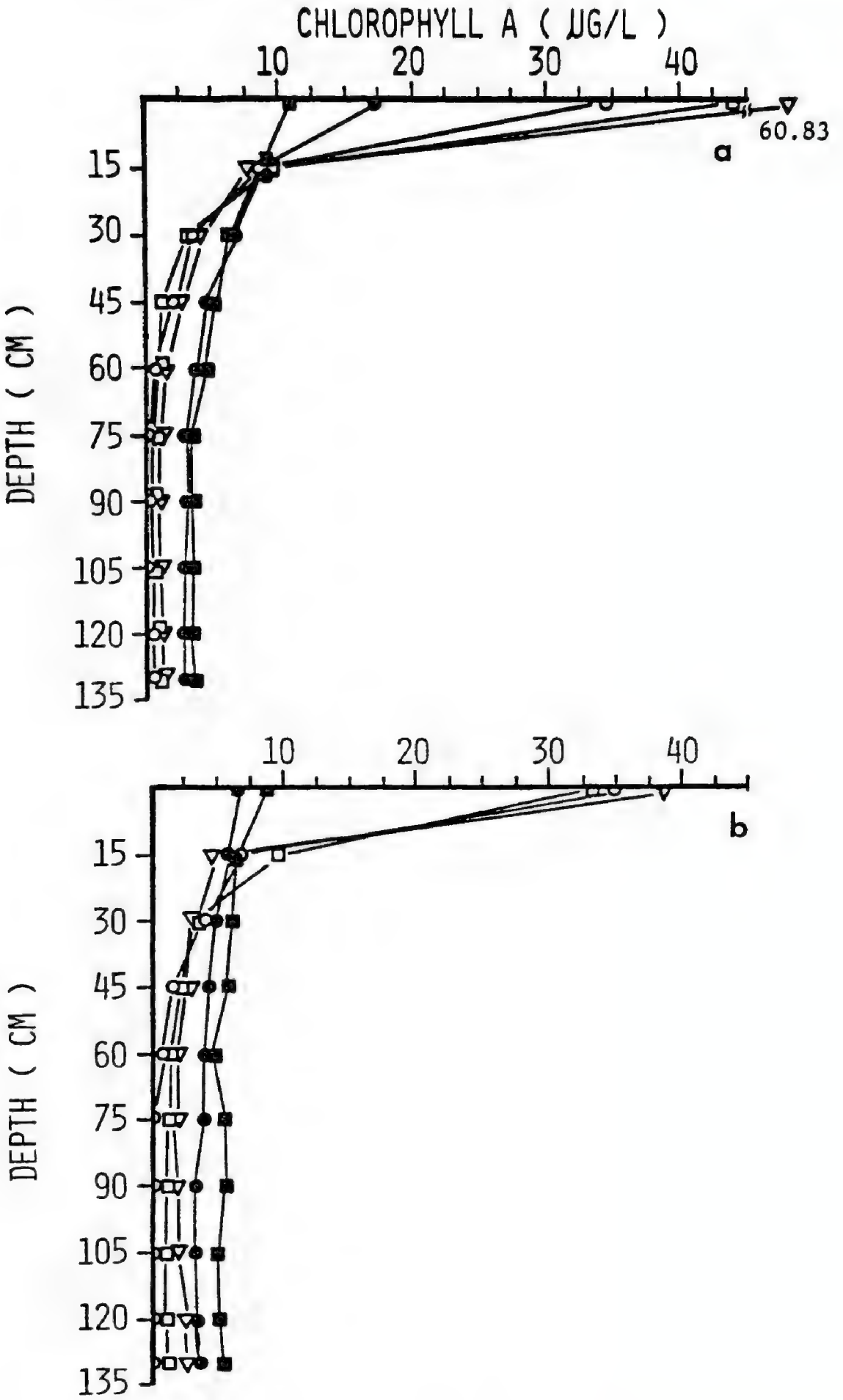


FIG. 3. Experiment 2. Chlorophyll *a* distributions in (a) column with *T. turbinata* adults and (b) column with *T. turbinata* copepodites. See caption Fig. 1 for explanation of symbols.

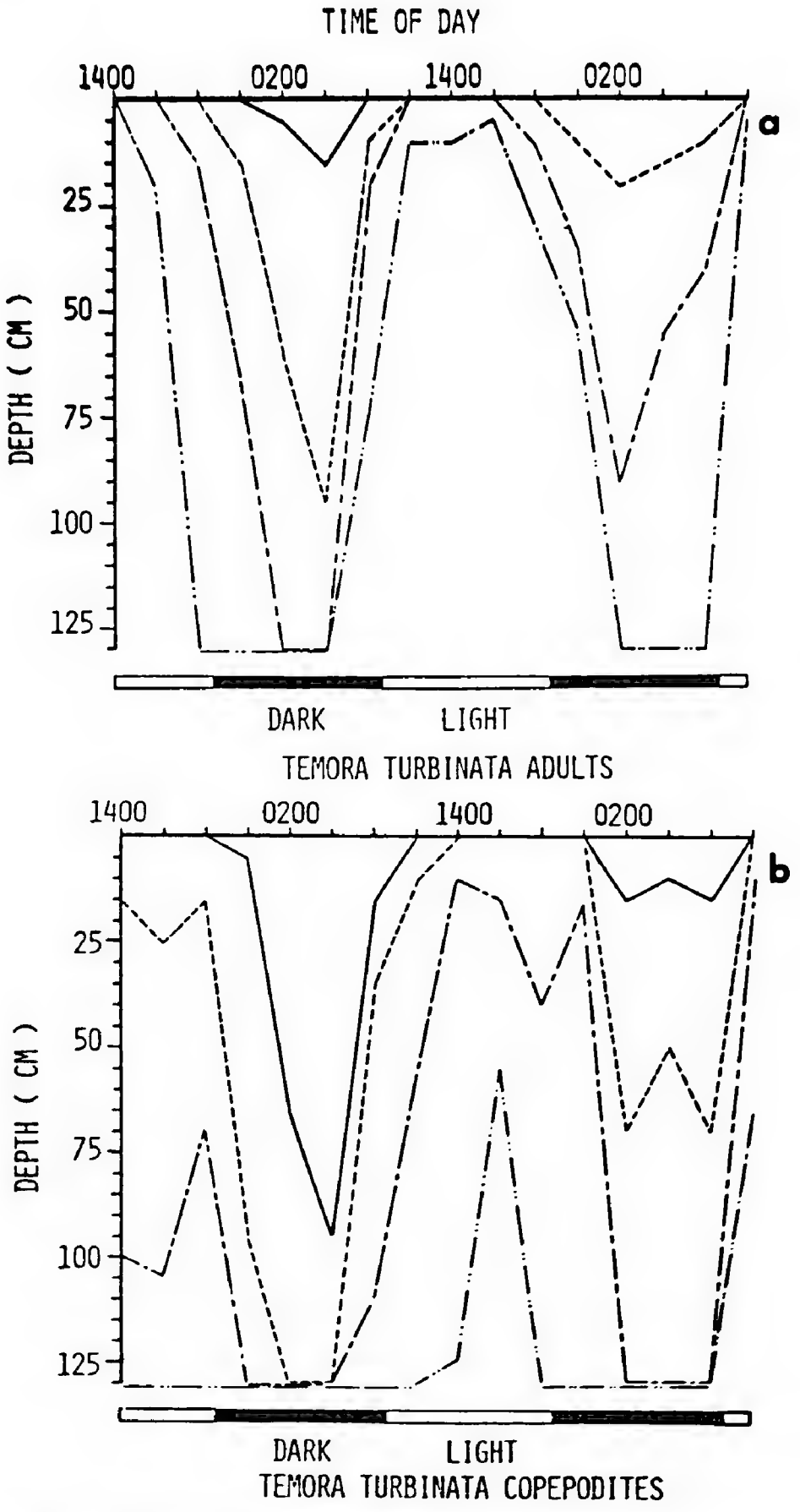


FIG. 4. Experiment 2. Distributions of *T. turbinata* (a) Adults (b) Copepodites. See caption for Fig. 2 for explanation of the symbols.

rapidly (Fig. 7a,b), which allowed comparison of adult and copepodite distributions in contrasting environments.

Adults were distributed similarly to those in previous experiments with *P. micans* but the depth of the 60th percentile varied more than the other

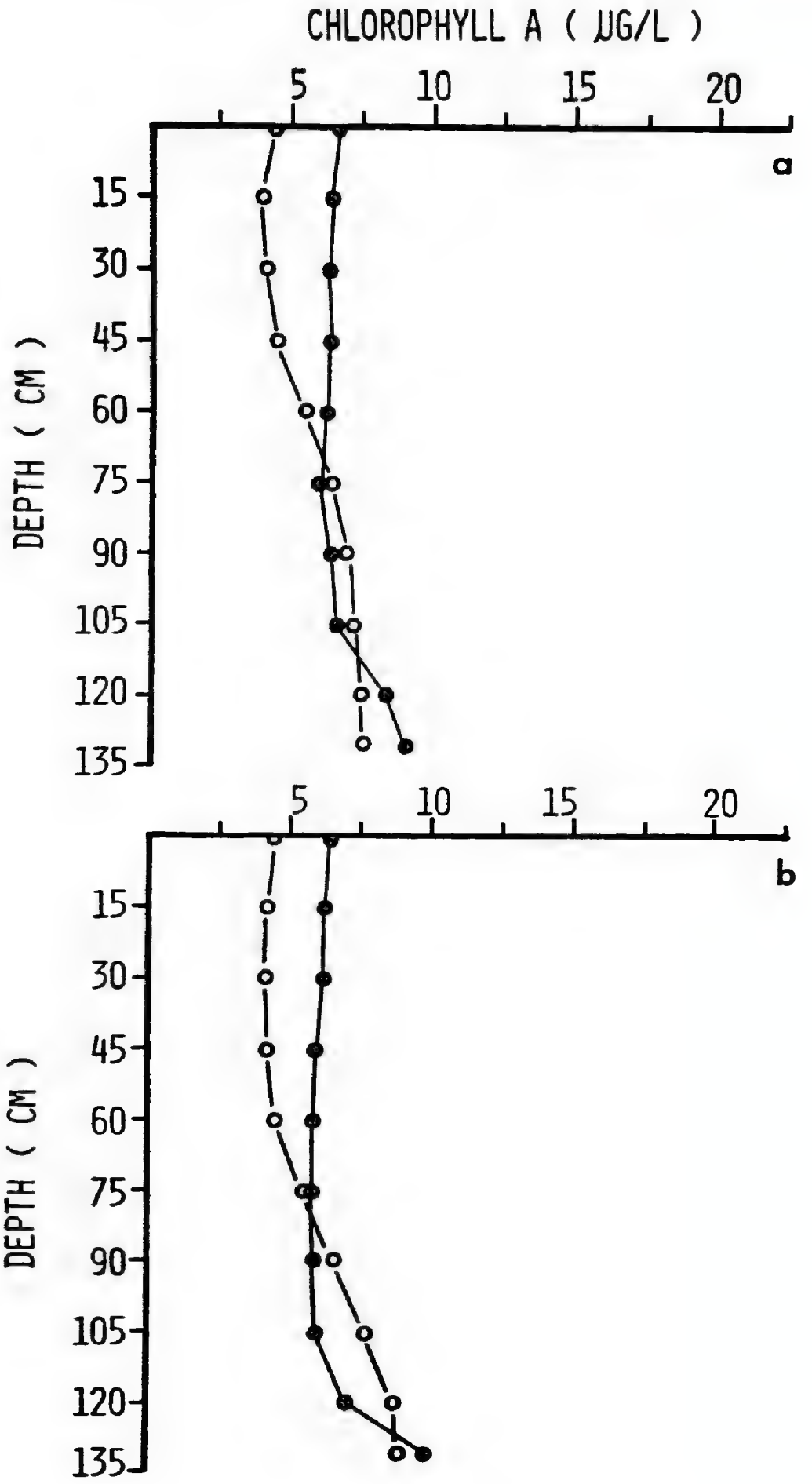


FIG. 5. Experiment 3. Chlorophyll *a* distributions of *C. niei* in columns with *T. turbinata* (a) adults and (b) copepodites. Open circles represent daytime and closed circles represent nighttime profiles.

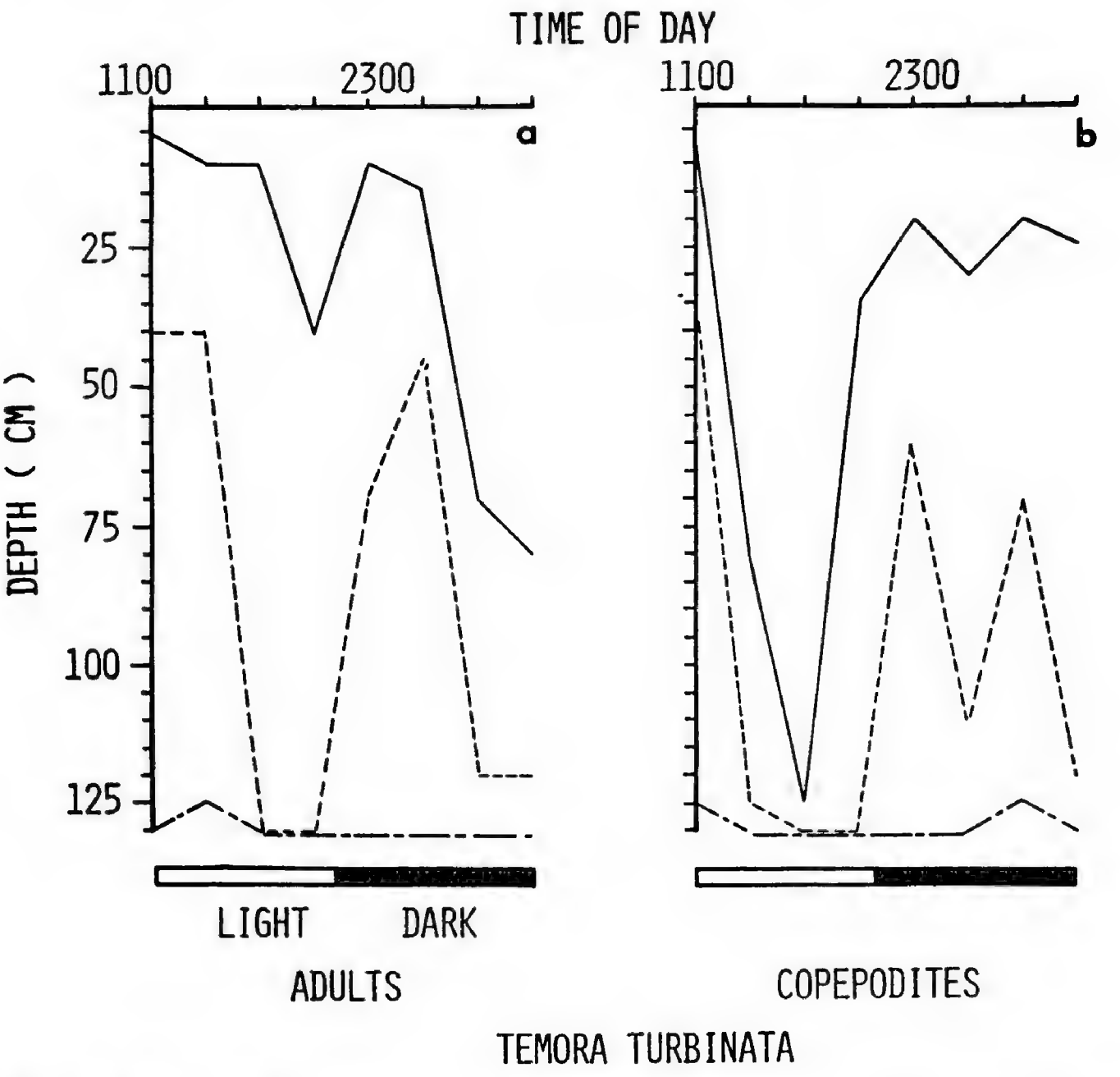


FIG. 6. Experiment 3. Distributions of *T. turbinata.* (a) adults and (b) copepodites. See caption for Fig. 2 for explanation of the symbols.

percentiles during the day (Fig. 8a). Day and night distributions were significantly different ($P < 0.01$).

In the column containing the copepodites, the introduced diatoms grew rapidly throughout the column. Initially, copepodites descended late in the day as in the preceding experiments. The copepodite distribution pattern reversed by the second day (Fig 8b). Adult and copepodite distributions differed during the day ($P < 0.01$).

**Experiment 5.** Adults and copepodites with low concentrations of *P. micans.*

Chlorophyll *a* concentrations and gradients were lowest in this experiment (Fig. 9a,b). In addition, the chlorophyll *a* concentration in the water column declined over the course of the experiment. In other experiments, chlorophyll *a* concentrations remained the same or increased. The decrease

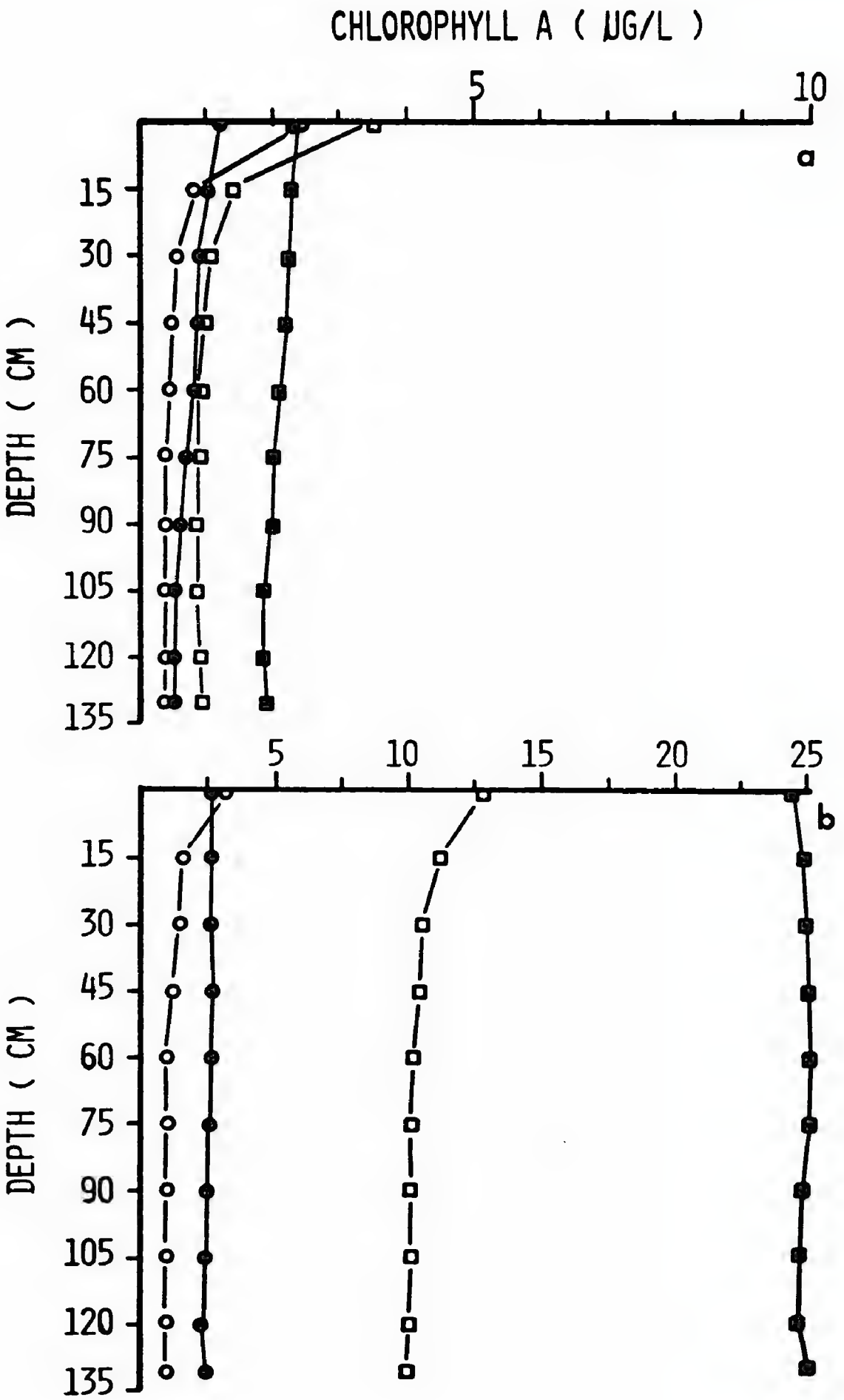


FIG. 7. Experiment 4. Chlorophyll *a* distributions in columns with *T. turbinata* (a) adults and (b) copepodites. See caption for Fig. 1 for explanation of symbols.

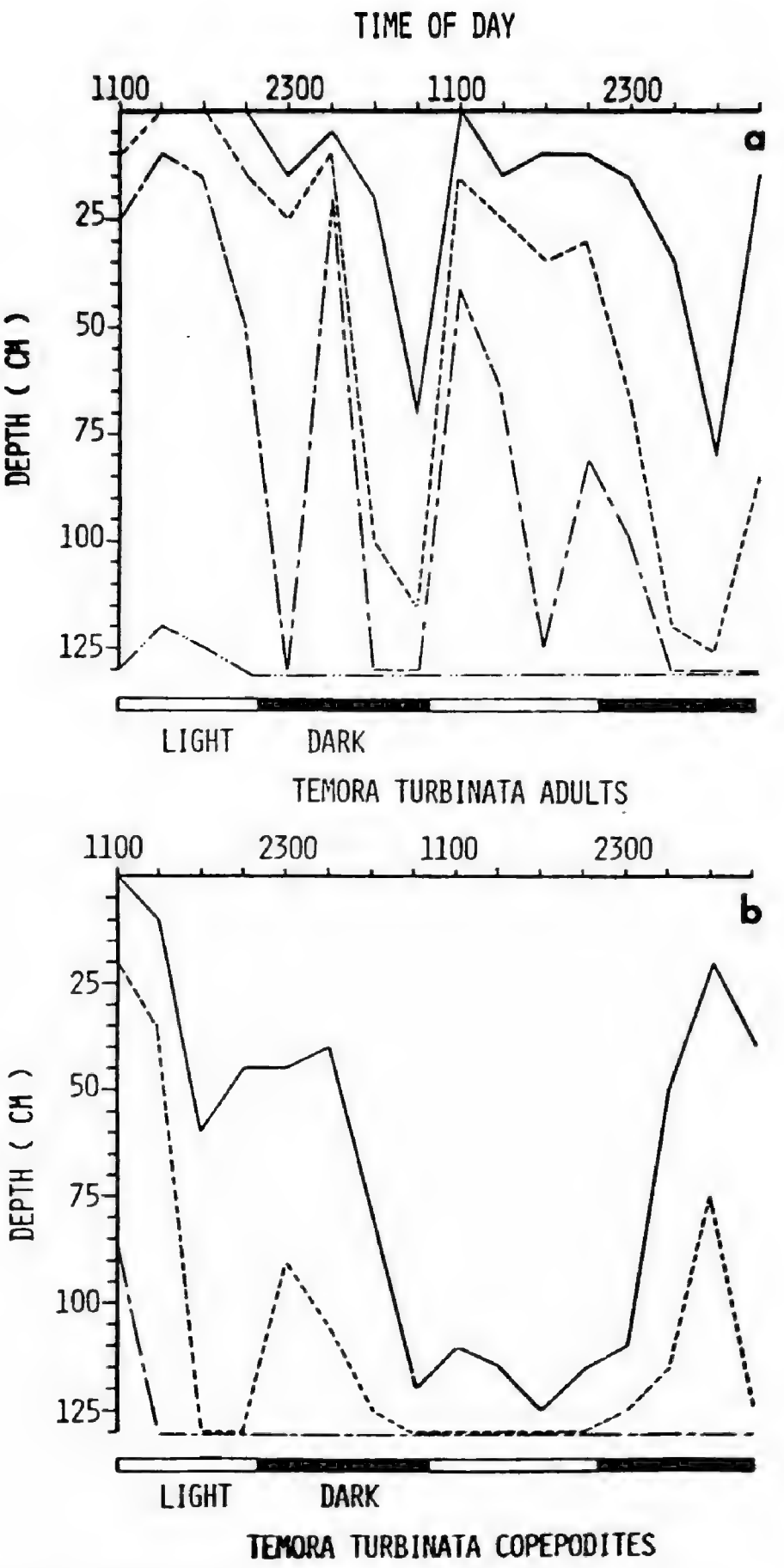


FIG. 8. Experiment 4. Distributions of *T. turbinata* (a) adults and (b) copepodites. See caption for Fig. 2 for explanation of the symbols.

in chlorophyll *a* concentrations suggested that either the phytoplankton sank or *T. turbinata* (1 to 2 animals/1) reduced the phytoplankton populations by grazing. Phaeophytin/ chlorophyll *a* ratios in this experiment were greater than 2, unlike the low P/C ratios (<0.50) of the other experiments. In

contrast to the other experiments, there was little diel variation in the chlorophyll *a* distributions.

Adult distributions illustrated two behavior patterns. (Fig. 10a). Over 40% of the population remained shallow in the day and displayed *T. turbinata*'s usual pattern of migration. Several animals, represented by the 60th percentile, remained deeper in the water column and moved over a greater range of depths during the day than the shallower portion of the population did. This movement occurred at depths where there was little variation in chlorophyll *a* concentration. A lack of significant differences between day and night distributions apparently resulted from variation in the depth of the deeper animals.

Copepodites exhibited the same migration pattern as the adults (Fig. 10b). However, a greater portion of the copepodites remained near the surface in the day and descended less at night than the adults. Several copepodites, represented by the 80th percentile, exhibited a pattern similar to the deeper adults. Copepodite day and night distributions were significantly different ($P < 0.01$) but copepodite and adult distributions did not exhibit significant differences either day or night.

## DISCUSSION

Laboratory studies in water columns indicate how variations in environmental conditions affect herbivore distribution and behavior. Previous laboratory studies attempted to analyze the role of light and temperature in vertical migration (Clarke 1930, Harris and Wolfe 1955, Conover 1956, McNaught and Hasler 1964, Ringelberg 1964). The present study demonstrates effects of phytoplankton distributions on copepod distributions.

*T. turbinata* exhibited a "reverse diel vertical migration" in the presence of the migratory dinoflagellate *P. micans*. Both adults and older copepodites migrated. This migration was characterized by a strong ascent to the surface in the morning, followed by a shallow descent in the afternoon and a more pronounced descent at night.

Bohrer (1980) also investigated the effects that phytoplankton distributions have on copepod distributions. In his study, a congeneric copepod, *T. longicornis*, rose steadily during the day, drifted downward slightly most of the night, and descended precipitously near dawn. Differences between the migration patterns of the two copepods were probably due to use of a migratory dinoflagellate, *P. micans* in the present study and a nonmigratory diatom in Bohrer's study. The nocturnal descent of *P. micans* would provide stimulus for *T. turbinata*'s descent. Differences between the two copepod species and sizes of the respective water columns also could have contributed to differences in migratory patterns.

During some of the experiments of the present study, descent of individuals within the population was not synchronous. Possibly, these differences resulted from descent of satiated animals or were the result of an increase in the depth searched by the copepods during phytoplankton vertical migra-

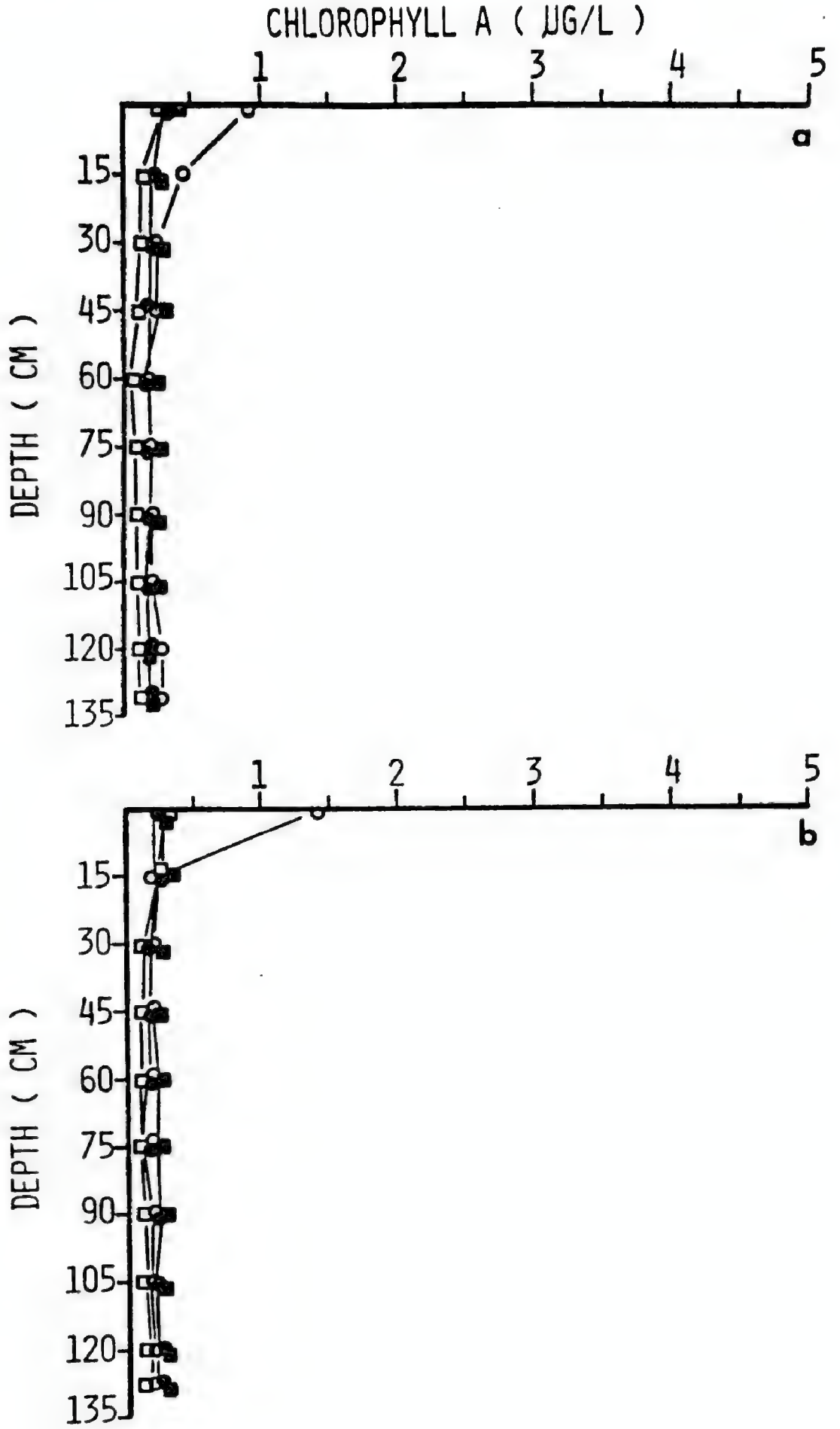


FIG. 9. Experiment 5. Chlorophyll *a* distributions in columns with *T. turbinata* (a) adults and (b) copepodites. See caption for Fig. 1 for explanation of symbols.

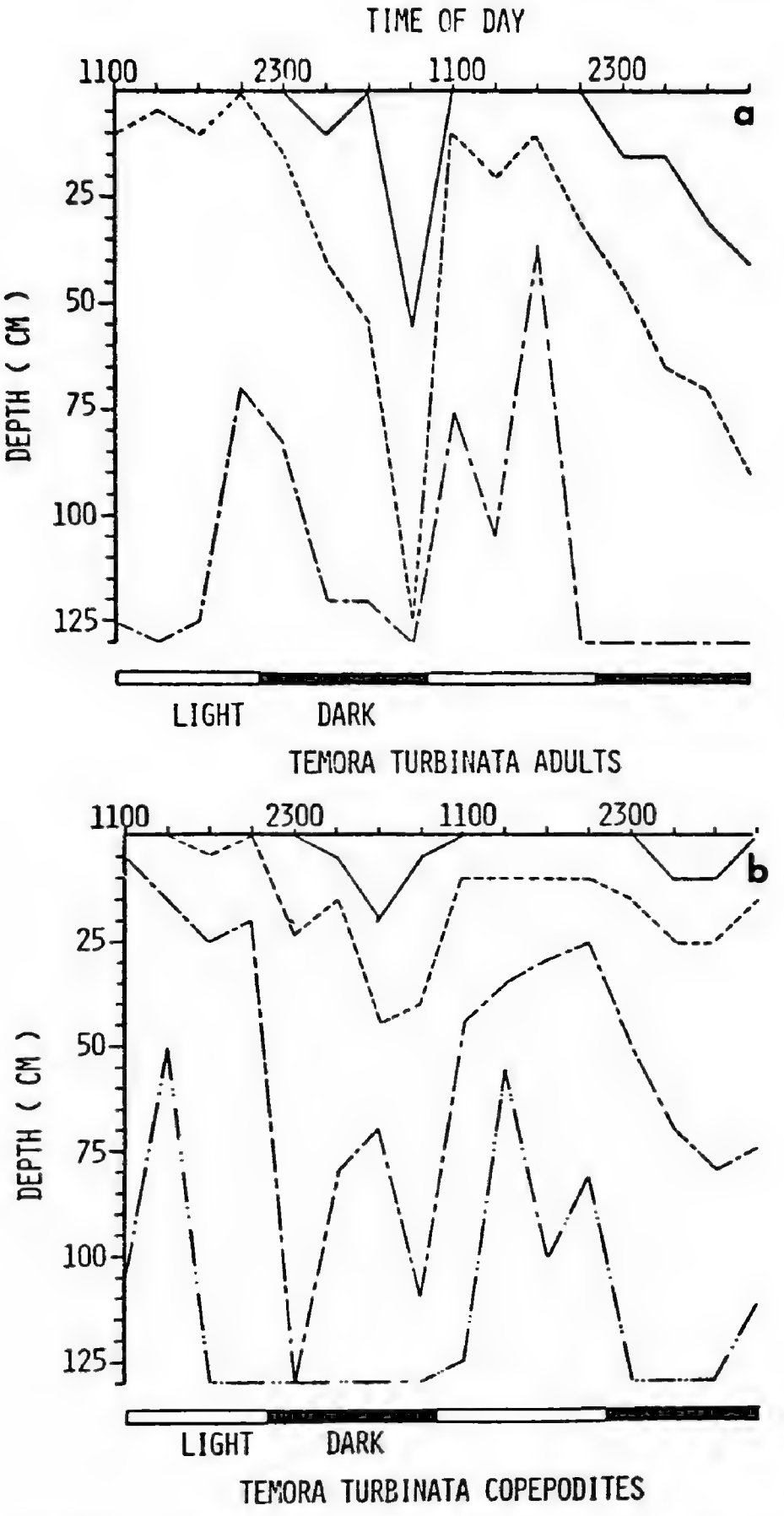


FIG. 10. Experiment 5. Distributions of *T. turbinata* (a) adults (b) copepodites. See caption for Fig. 2 for explanation of symbols.

tion. The former seems more probable although no direct evidence of satiation was obtained. Bohrer (1980) also reported inconclusive results of satiation effects on vertical migration.

Mackas and Bohrer (1976) and Pearre (1979) reported that satiated animals in the sea descended earlier than unsatiated animals. Pearre (1979) suggested that asynchrony in migration due to descent of satiated animals could result in the apparent lack of migration when in reality the population was feeding near the surface. Singarajah *et al.* (1967) have shown that the recent feeding history of many planktonic animals may cause changes in their phototactic responses.

In one experiment (Bird 1981) migration was not apparent from the distribution of the copepods. This experiment could be interpreted as asynchronous migration due either to satiation effects on individuals or to true nonmigration. Daytime distributions of several dyed animals during that experiment showed that individuals would occasionally move through the water column and not be synchronized with movement of other individuals. We were unable to determine the distribution of the red-dyed copepods at night due to the red filter on the flashlight. Observations of the swimming behavior of individuals indicated that *T. turbinata* could move the length of the column in less than 20 minutes.

When phytoplankton concentrated near the bottom, both adults and copepodites were found deeper in the column than they were when phytoplankton concentrated near the surface. These patterns were very similar to the observed distributions of several species in the Gulf of Mexico in June and July, 1978 (Bird 1981). In the absence of food in the laboratory, *T. turbinata* adults concentrated near the bottom of the water column.

*T. turbinata* seems well adapted to utilize phytoplankton distributions on the Texas continental shelf. During the fall, winter, and spring, phytoplankton biomass is concentrated near the surface or spread throughout the water column. When phytoplankton concentrated near the surface in the present study, *T. turbinata* was often found near the surface during the day. During periods of water column stratification on the Texas continental shelf, phytoplankton was generally abundant near the bottom, (Kamykowski and Bird 1981). In the laboratory, *T. turbinata* descended in the presence of subsurface chlorophyll *a* maxima or absence of food. This behavior would enable it to locate deep chlorophyll *a* layers encountered on the Texas continental shelf.

In the sea, amplitudes of herbivore migrations are not as restricted by water depth as in the laboratory but may be restricted by phytoplankton migration rates, up to 1–2 m/h (Kamykowski and Zentara 1977). In the sea, *T. turbinata* was distributed similarly to phytoplankton (Bird 1981). In the laboratory, *T. turbinata* is capable of altering its distribution to take advantage of phytoplankton heterogeneity. This behavior supports theories of planktonic distributions based on resource utilization. Predation has not been ruled out as a strong modifier of zooplankton distributions. Only further experimentation will resolve this point. Additionally, the importance of visual (vertebrate) versus nonvisual (invertebrate) predation must be determined in the environment.

## CONCLUSIONS

1. When phytoplankton concentrated at the surface, the usual migration pattern for *T. turbinata* was a morning ascent and an evening descent.
2. When food was absent or concentrated near the bottom, *T. turbinata* was found deeper in the water column. Under these conditions, a portion of the population was shallower at night than in the day.
3. *T. turbinata* surveyed more of the column when phytoplankton concentrations were low than when they were high.

## ACKNOWLEDGMENTS

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## LITERATURE CITED

BIRD, J. L. 1981. Relationships between vertical distributions of zooplankton and phytoplankton on the Texas continental shelf and in laboratory water columns. Ph.D. dissertation Univ. of Texas at Austin. pp. 148.

BOHRER, R. N. 1980. Experimental studies on diel vertical migration. Pages 11–121. In W. C. Kerfoot (ed) *Evolution and Ecology of Zooplankton Communities.* Univ. Press of New England, Hanover, N.H.

BOOKER, M. J., M. T. DINSDALE, and and A. E. WALSBY. 1976. A continuously monitored column for the study of stratification by planktonic organisms. *Limnology and Oceanography.* 21:915–919.

CLARKE, G. L. 1930. Change in phototrophic and geotropic signs in *Daphnia* induced by changes of light intensity. *Journal of Experimental Biology.* 7:109–131.

CONOVER, R. J. 1956. Oceanography of Long Island Sound. VI. Biology of *Acartia clausi* and *A. tonsa. Bulletin of the Bingham Oceanographic Collection.* 15:156–233.

ENRIGHT, J. T. 1977. Diurnal vertical migration: adaptive significance and timing. Part 1. Selective advantage: a metabolic model. *Limnology and Oceanography.* 22:856–872.

FLEMINGER, A. 1956. Taxonomic and distributional studies of the epiplanktonic calanoid copepods (Crustacea) of the Gulf of Mexico. Ph.D. dissertation Harvard Univ. pp. 317.

HARRIS, J. E. and U. K. WOLFE. 1955. A laboratory study of vertical migration. *Proceedings of the Royal Society of London. Series B.* 144:329–354.

HEANEY, S. T. and R. W. EPPLEY. 1981. Light, temperature, and nitrogen as interacting factors affecting diel vertical migrations of dinoflagellates. *Journal of Plankton Research.* 3:331–344.

KAMYKOWSKI, D. 1976. Possible interactions between plankton and semi-diurnal internal tides: II. Deep thermocline and trophic effects. *Journal of Marine Research.* 34:399–409.

_____. 1981. Laboratory experiments on diurnal vertical migration of marine dinoflagellates through temperature gradients. *Marine Biology.* 62:57–64.

_____ and J. L. BIRD. 1981. Phytoplankton associations with the variable nepheloid layer on the Texas continental shelf. *Estuarine, Coastal, and Shelf Science.* 13:317–326.

_____ and S.-J. ZENTARA. 1977. The diurnal vertical migration of motile phytoplankton through temperature gradients. *Limnology and Oceanography.* 22:148–151.

LOEBLICH, A. R. III. 1975. A seawater medium for dinoflagellates and the nutrition of *Cachonina niei*. *Journal of Phycology*. 11:80–86.

MACKAS, D. and R. BOHRER. 1976. Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *Journal of Experimental Marine Biology and Ecology*. 25:77–85.

McLAREN, I. A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *Journal of the Fisheries Research Board of Canada*. 20:685–727.

———. 1974. Demographic strategy of vertical migration in marine zooplankton. *American Naturalist*. 108:91–102.

McNAUGHT, D. C. and A. D. HASLER. 1964. Rate of movement of populations of *Daphnia* in relation to changes in light intensity. *Journal of the Fisheries Research Board of Canada*. 21:291–316.

NARVER, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine lake, British Columbia. *Journal of the Fisheries Research Board of Canada*. 27:281–316.

PEARRE, S., JR. 1979. Problems of detection and interpretation of vertical migration. *Journal of Plankton Research*. 1:29–44.

RAYMONT, J. E. G. 1980. *Plankton and productivity in the oceans*. 2nd ed. Vol. 1. *Phytoplankton*. Pergamon Press. New York. pp. 489.

RINGELBERG, J. 1964. The positively photoactic reaction of *Daphnia magna* Straus. *Netherlands Journal of Sea Research*. 2:319–406.

SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Book Co., Inc. New York. 312 pp.

SINGARAJAH, K. V., J. MOYSE and E. W. KNIGHT-JONES. 1967. The effect of feeding upon the phototactic behavior of cirripede nauplii. *Journal of Marine Biology and Ecology*. 1:144–153.

STRICKLAND, J. D. H. and T. PARSONS. 1968. A practical handbook of seawater analysis. *Bulletin, Fisheries Research Board of Canada*. 167:311.

ZARET, T. M. and J. S. SUFFERN. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnology and Oceanography*. 21:804–813.

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# SHALLOW WATER MARINE ISOPODS OF TEXAS

Scott T. Clark[1] and Philip B. Robertson[2]

*Department of Biology, Lamar University, Beaumont, Texas*

[1]Present address: 1012 Sunset Circle West, Yale, Oklahoma 74085
[2]Present address: 9218 Braswell, San Antonio, Texas 78250

## ABSTRACT

The occurrence and distribution of isopod crustaceans in marine and estuarine waters of Texas was investigated by examination of specimens obtained from a variety of habitats from the intertidal to 98 m depth offshore. Thirty free-living and seven ectoparasitic species are recorded. An illustrated key is included to facilitate identification. Four (possibly five) are apparently undescribed species and 15 represent range extensions to Texas. Three of the described species are known only from Texas. Few species were numerically abundant, and rarely were more than three species found in a single collection at any given habitat. The Texas isopod fauna shows its greatest affinity to the North Atlantic coast south of Cape Hatteras. A small group of more or less strictly tropical species inhabits deeper offshore banks and reefs off the Texas coast.

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## INTRODUCTION

Isopod crustaceans are found in a variety of benthic habitats and less commonly in plankton. There have been no comprehensive attempts to study the isopod fauna of the northern Gulf of Mexico; consequently little is known of the occurrence and distribution of the species in this region. Only a few of the more common species have been recorded in ecological surveys of the Texas coast (*e.g.*, Breuer 1962; Hedgpeth 1953; Simmons 1957; Whitten, Rosene and Hedgpeth 1950). Gillespie (1969) reported six species from the Mississippi delta, and Pearse (1952) treated parasitic species from the Texas coast. Several species were recorded from Texas in an unpublished preliminary survey by Duplechin and Callahan (1975). Other publications dealing with isopods from the Texas coast are limited to a few new species descriptions and range extensions (Menzies 1951; Menzies and Miller 1955; Harper 1974; Callahan, Clark and Robertson 1977; Robertson 1978). Regional guides are available for Georgia (Menzies and Frankenberg 1966) and for Puerto Rico (Menzies and Glynn 1968). Watling, Lindsay, Smith, and Maurer (1974) listed species from Delaware Bay.

The present study was undertaken to determine the occurrence and distribution of marine and estuarine isopods in Texas and to facilitate identification of the regional fauna.

## MATERIALS AND METHODS

We deal herein with free-living and ectoparasitic isopods but do not include the highly specialized parasites of the Suborder Epicaridea (Bopyroidea). It should be noted, though, that the minute larval and juvenile stages (epicaridium, microniscium, cryptoniscium) of this group may be free-living.

Isopods were collected from a wide variety of habitats in marine and estuarine areas of Texas from the intertidal zone to 98 m depth offshore. Sporadic collections were made at different times at a total of 142 inshore stations from Sabine Pass to South Padre Island during July 1976 to April 1978. Temperature, salinity, and substrate type were recorded at each site. Marine grasses, algae, and plankton tows were preserved in the field and later sorted in the laboratory. Sediments of beaches and mudflats were sieved. The formalin bucket technique (Menzies and Glynn 1968) was used to collect material from rocks and oyster clumps covered with encrusting growths. Larger specimens found individually by examining rocks, pieces of wood, and other hard substrates were placed directly into a solution of 70 percent ethanol, 20 percent glycerin, and 10 percent water, as were other specimens after sorting. Various fishes were collected by seining and trawling and examined for ectoparasitic isopods. In addition to personal collections and some previously collected museum specimens, we examined offshore and some additional inshore materials generously provided by other investigators. These materials included specimens from the Buccaneer Oil Field spoil area offshore from Galveston; the intake screens at the Barney Davis power plant, Corpus Christi; offshore during the Bureau of Land Management South Texas Outer Continental Shelf Monitoring Study (UTMSI); from offshore banks, rocks, and the Flower Garden coral reefs (TAMU); and from the upper Laguna Madre near marker 41.

We examined and verified all species recorded here with the exception of two ectoparasites reported from Texas by Pearse (1952). In the brief account of each species, reference is made immediately after the figure number following the species name to a descriptive source used for identification. Annotations describing distribution and abundance refer to habitats in which the species has been collected in Texas. Total length is indicated as TL. An artificial key illustrated with original figures is included as an aid to ecologists and students in identifying isopods encountered on the Texas coast. All scales accompanying the figures indicate millimeters.

## AN ARTIFICIAL KEY TO MARINE AND ESTUARINE ISOPODS OF TEXAS

1a. Uropods inserted on antero-lateral margin of pleotelson (Fig. 1), (may be folded ventrally under the pleotelson) ..... 2
1b. Uropods inserted on or near posterior border of pleotelson; usually styliform (Fig. 2) (may or may not extend beyond posterior margin of pleotelson) .... 31
2a. Uropods flattened and folded ventrally under the pleotelson, forming a chamber enclosing the pleopods (Suborder Valvifera)..... 3
2b. Uropods not folded ventrally under the pleotelson ..... 9
3a. Fourth pereonite much longer than the other pereonites..... .....*Astacilla lauffi* (Fig. 3).
3b. Fourth pereonite not much longer than the other pereonites..... 4
4a. Eyes located dorsally; antenna 1 and antenna 2 subequal ..... .....*Chiridotea excavata* (Fig. 4).
4b. Eyes lateral or dorso-lateral; antenna 1 and antenna 2 not subequal ..... 5
5a. Antenna 2 with multiarticulate flagellum .....*Synidotea* sp. (Fig. 5).
5b. Antenna 2 flagellum of three or fewer articles..... 6
6a. Antenna 2 only slightly longer than antenna 1.....*Edotea montosa* (Fig. 6).
6b. Antenna 2 at least 4 times longer than antenna 1..... 7
7a. Pleon with 2 or 3 free pleonal somites.....*Cleantis planicauda* (Fig. 7).
7b. Pleon composed of pleotelson only; no free pleonal somites..... 8

8a. Epistome bifid; an elevated protuberance dorsally on cephalon..... .....*Erichsonella filiformis isabelensis* (Fig. 8).
8b. Epistome with a single point; dorsum of cephalon slightly elevated and rounded .....*Erichsonella attenuata* (Fig. 9).
9a. Five pairs of pereopods; mandibles in male large and projecting anteriorly past front margin of cephalon (Suborder Gnathioidea) ..... *Gnathia* sp. (Fig. 10).
9b. Seven pairs of pereopods; mandibles in male not produced anteriorly..... 10
10a. Body six to seven times longer than wide; uropodal exopod folds over the pleotelson (Suborder Anthuridea)..... 11
10b. Body less than six times longer than wide; uropods flattened, forming a tail-fan with the pleotelson, or tubular and located laterally under edge of pleotelson.....(Suborder Flabellifera) ..... 13
11a. Eyes absent; pleotelson apex acutely pointed or narrowly rounded..... 12
11b. Eyes present (male with 3 pairs); pleotelson apex truncate ..... .....*Xenanthura brevitelson* (Fig. 11).
12a. Pleotelson apex acutely pointed; uropodal exopod with 3 stout spines medially .....*Horoloanthura irpex* (Fig. 12).
12b. Pleotelson apex narrowly rounded; uropodal exopod without spines..... .....*Anthelura* sp. (Fig. 13).
13a. Pleon composed of 3 or fewer free somites plus pleotelson ..... 14
13b. Pleon composed of 4 or 5 free somites plus pleotelson ..... 20
14a. Uropods uniramous, consisting of a single styliform endopod ..... .....*Ancinus depressus* (Fig. 14).
14b. Uropods biramous ..... 15
15a. Uropodal exopod short and inset into lateral margin of endopod..... .....*Cassidinidea ovalis* (Fig. 15).
15b. Uropodal exopod about as long as or longer than endopod and not inset into latter ..... 16
16a. Uropodal exopod with 4 to 9 stout teeth on lateral margin..... 17
16b. Uropodal exopod margin crenulate or smooth ..... 18
17a. Dorsum of pleotelson smooth or with a few tubercles in males ..... .....*Sphaeroma quadridentatum* (Fig. 16).
17b. Dorsum of pleotelson with 4 longitudinal rows of tubercles..... .....*Sphaeroma walkeri* (Fig. 17).
18a. Uropodal exopod acutely pointed, longer than endopod ..... .....*Cymodoce faxoni* (Fig. 18).
18b. Uropodal rami apically rounded, subequal..... 19
19a. Pleotelson dorsum lacking tubercles; posterior margin of pleotelson smoothly rounded in both sexes.....*Exosphaeroma productatelson* (Fig. 19).
19b. Pleotelson dorsum with 4 tubercles in a trapezoidal pattern; pleotelson apex in adult male with a heart-shaped foramen.....*Dynamenella dianae* (Fig. 20).
20a. Uropods tubular, with at least one hook-like ramus..... .....*Limnoria (Limnoria) tripunctata* (Fig. 21).
20b. Uropodal rami both flattened..... 21
21a. All pereopods prehensile; both antennae reduced, lacking a clear distinction between peduncle and flagellum ..... 22
21b. Pereopods either ambulatory and prehensile or all ambulatory; a clear distinction between antennae peduncle and flagellum ..... 28
22a. Posterior margins of uropods and pleotelson fringed with fine setae ..... 23
22b. Posterior margins of uropods and pleotelson not fringed with setae..... 24
23a. Frontal margin of cephalon with a broad lingulate rostral projection..... .....*Aegathoa medialis* (Fig. 22).
23b. Frontal margin of cephalon smoothly rounded, without a lingulate rostral projection .....*Aegathoa oculata* (Fig. 23).
24a. Eyes absent ..... *Cymothoa oestrum.*

24b. Eyes present ..... 25
25a. Cephalon as long as wide, not inset into first pereonite; pereopod VII much longer than other pereopods ..... *Olencira praegustator* (Fig. 24).
25b. Cephalon wider than long; pereopod VII not much longer than other pereopods ..... 26
26a. Postero-lateral angles of pereonites VI and VII much produced; uropods extend past posterior border of pleotelson ..... *Nerocila acuminata* (Fig. 25).
26b. Postero-lateral angles of pereonites VI and VII not produced; uropods do not extend beyond posterior border of pleotelson ..... 27
27a. Pleon width about one-half width of pereon; apex of pleotelson acutely tapering ..... *Anilocra laticauda.*
27b. Pleon about as wide as pereon; apex of pleotelson broadly truncate..... ..... *Livoneca texana* (Fig. 26).
28a. Dorsum of pleotelson with a median groove having a thick hirsute area on each side; lateral margin of pleotelson incised.... *Excorallana antillensis* (Fig. 27).
28b. Dorsum of pleotelson not as above; pleotelson margin not incised ..... 29
29a. Posterior margin of pleotelson with 4 stout setae; peduncle basal article of antenna 1 at right angles to second article ..... *Eurydice littoralis* (Fig. 28).
29b. Posterior margin of pleotelson without stout setae, or with more than 4; peduncle basal article of antenna 1 not as above..... 30
30a. Posterior margin of pleotelson with several stout setae; lateral margin of uropodal endopod without a distinct spine ..... *Cirolana parva* (Fig. 29).
30b. Posterior margin of pleotelson crenulate, lacking stout setae; lateral margin of uropodal endopod with a distinct spine ..... *Cirolana mayana* (Fig. 30).
31a. Antenna 1 rudimentary, composed of 2 or 3 short articles; pleon composed of 5 free somites plus pleotelson...(Suborder Oniscoidea) .. *Ligia exotica* (Fig. 31).
31b. Antenna 1 not rudimentary, composed of more than 4 articles; pleon composed of fewer than 3 somites plus pleotelson.....(Suborder Asellota) ..... 32
32a. Both antennae very short, folding against frontal margins of cephalon (Fig. 32) 36
32b. Antennae not as above..... 33
33a. Eyes on short protuberances at extreme lateral margins of cephalon; uropods not projecting noticeably beyond posterior margin of pleotelson; TL about 1 mm 34
33b. Eyes located dorso-laterally on cephalon; uropods projecting beyond posterior margin of pleotelson ..... 35
34a. First pleopods of male not expanded distally; postero-lateral margins of pleotelson with indentations for uropods, which extend slightly beyond the margin ..... *Munna (Uromunna) reynoldsi* (Fig. 33).
34b. First pleopods of male expanded distally; postero-lateral margins of pleotelson without indentations for uropods, which do not extend beyond the margin .. ..... *Munna (Uromunna) hayesi* (Fig. 34).
35a. Pleotelson with a spine or tooth on lateral border; antenna 1 longer than antenna 2 ..... *Stenetrium occidentale* (Fig. 35).
35b. Pleotelson lateral margins lacking a spine or tooth; antenna 2 longer than antenna 1 ..... *Janira minuta* (Fig. 36).
36a. Epistome shallowly indented; lateral margins of pleotelson serrated..... ..... *Jaeropsis* sp. A (Fig. 37).
36b. Epistome rounded; lateral margins of pleotelson not serrated ..... ..... *Jaeropsis* sp. B. (Fig. 38).

## SPECIES ACCOUNTS

Lists of the species recorded and their habitat associations are given in Tables 1 and 2.

TABLE 1

**Isopod species recorded from Texas and their known ranges.**

| | |
|---|---|
| **Aegathoa medialis* | Chesapeake and Delaware Bays; Texas |
| *Aegathoa oculata* | Connecticut to West Indies and Yucatan |
| *Ancinus depressus* | Massachusetts to Texas |
| *Anilocra laticauda* | Maryland to Straits of Magellan |
| *Anthelura* sp. | Texas |
| **Astacilla lauffi* | Georgia; Texas |
| *Cassidinidea ovalis* | New Jersey to Florida and Texas |
| *Chiridotea excavata* | Texas |
| **Cirolana mayana* | Puerto Rico, Yucatan, Texas; California |
| **Cirolana parva* | Georgia, Texas, the Caribbean; Indian and Pacific Oceans |
| **Cleantis planicauda* | Georgia and Gulf of Mexico to Puerto Rico |
| *Cymodoce faxoni* | Florida and Texas |
| *Cymothoa oestrum* | Virginia to Venezuela |
| **Dynamenella dianae* | Puerto Rico; Texas; California |
| *Edotea montosa* | Nova Scotia to Florida and Texas |
| **Erichsonella attenuata* | Connecticut to North Carolina; Texas |
| *Erichsonella filiformis* | Massachusetts to Florida and Texas |
| **Eurydice littoralis* | Georgia and Texas to Puerto Rico |
| **Excorallana antillensis* | Florida and Texas to Puerto Rico |
| **Exosphaeroma productatelson* | Puerto Rico; Texas (stranding?) |
| *Gnathia* sp. | Texas |
| **Horoloanthura irpex* | Georgia; Texas |
| *Jaeropsis* sp. A. | Texas |
| *Jaeropsis* sp. B. | Uncertain |
| *Janira minuta* | Bermuda; Atlantic and Gulf coasts, on *Sargassum* |
| *Ligia exotica* | North Carolina to Brazil; Pacific |
| *Limnoria tripunctata* | Rhode Island to Venezuela; San Francisco to Mazatlan, Mexico |
| *Livoneca texana* | Texas |
| *Munna hayesi* | Texas |
| *Munna reynoldsi* | Georgia to Texas |
| *Nerocila acuminata* | Virginia to Mexico |
| *Olencira praegustator* | New Jersey to Texas |
| *Sphaeroma quadridentatum* | Nova Scotia to Florida and Texas |
| **Sphaeroma walkeri* | Pantropical; Florida and Texas to Brazil in this hemisphere |
| **Stenetrium occidentale* | Bermuda; Puerto Rico and West Indies; Texas |
| *Synidotea* sp. | Texas |
| **Xenanthura brevitelson* | Georgia and Texas to West Indies |

*indicates range extension to Texas

## SUBORDER VALVIFERA

### Family Arcturidae

***Astacilla lauffi*** Menzies and Frankenberg, 1966. Figure 3. Menzies and Frankenberg, 1966: p. 20–21, fig. 1. One female (TL 5.3 mm) from offshore at 65 m depth (UTMSI). Remarks: Previously known only from Georgia at 41 to 135 m depth.

### Family Idoteidae

***Chiridotea excavata*** Harper, 1974. Figure 4. Harper, 1974: p. 229–232, figs. 233–239. Occasional in the swash zone and surf of sandy beaches 3 km east of High Island and at San Luis

TABLE 2

**Habitat associations of isopod species recorded from Texas.**

Offshore Soft Bottoms, 3.5 to 98 m depth
- *Anthelura* sp. - silty clay
- *Astacilla lauffi* - predominantly sand
- *Chiridotea excavata* - sand
- *Gnathia* sp. - silty clay
- *Horoloanthura irpex* - sandy clay
- *Limnoria tripunctata* - silty clay (?accidental)
- *Munna hayesi* - predominantly sand
- *Xenanthura brevitelson* - predominantly sand

Flower Gardens Coral Reefs, 16 to 24 m depth
- *Cirolana mayana*
- *Cirolana parva*
- *Eurydice littoralis*
- *Steretrium occidentale*

Offshore Rocks and Banks to 68 m depth
- *Cirolana mayana*
- *Cirolana parva*
- *Excorillana antillensis*
- *Jaeropsis* sp. A.
- *Stenetrium occidentale*

Oyster Reefs
- *Cassidinidea ovalis*

Open Coast Sand Beaches
- *Ancinus depressus*
- *Chiridotea excavata*
- *Synidotea* sp.

Inshore Muddy-Sandy Flats
- *Xenanthura brevitelson*

Sargassum
- *Janira minuta*

Pilings and Driftwood
- *Exosphaeroma productatelson*
- *Ligia expotica*
- *Limnora tripunctata*
- *Sphaeroma quadridentatum*

Rock Jetties
- *Cleantis planicauda*[1]
- *Dynamenella dianae*
- *Jaeropsis* sp. B.
- *Ligia exotica*
- *Munna hayesi*
- *Sphaeroma quadridentatum*
- *Sphaeroma walkeri*

Seagrass and Algal Beds in Bays
- *Cyodoce foxoni*
- *Edotea montosa*
- *Erichsonella attenuata*
- *Erichsonella filiformis*

Brackish Coastal Lakes and Marshes
- *Cassidinidea ovalis*
- *Edotea montosa*
- *Munna reynoldsi*

Fish Ectoparasites
- *Aegathoa medialis*
- *Aegathoa oculata*
- *Anilocra laticauda*
- *Cymothoa oestrum*
- *Livoneca texana*
- *Nerocila acuminata*
- *Olencira praegustator*

[1]Beneath rock on sand bottom adjacent to jetty.

Pass; occurs also on sandy offshore bottoms from 3.5 to 8 m depth (Harper 1974). Remarks: Known only from the upper Texas coast.

*Cleantis planicauda* Benedict, 1899. Figure 7. Menzies and Frankenberg, 1966: p. 23, fig. 3. One specimen (TL 17.5 mm) from under a rock on intertidal sand near the south jetty at Port Aransas. Remarks: Reported to be a common inhabitant of *Diopatra cuprea* tubes in the northeastern Gulf of Mexico (Hooks *et al.* 1976).

*Edotea montosa* (Stimpson, 1853). Figure 6. Menzies and Frankenberg, 1966: p. 22, fig. 2. Several specimens from brackish marsh lakes (salinity 0 to 4.4 ppt) in Sea Rim State Park, and higher salinity bays (19 to 26 ppt) in central Texas south to Baffin Bay. Remarks: This species was found only at salinities greater than 25 ppt in the Delaware Bay region (Watling *et al.* 1974). Wallace (1919) suggested that it may be a high salinity form of the polyhaline *E. triloba* (Say); however, this does not appear to be the case on the basis of material from Texas.

*Erichsonella attenuata* (Harger, 1873). Figure 9. Richardson, 1905: p. 400–401, figs. 447–448. Common in seagrass and algae beds in southern Texas bays from Matagorda Bay to the lower Laguna Madre, at salinities from 7 to 35 ppt.

*Erichsonella filiformis isabelensis* Menzies, 1951. Figure 8. Schultz, 1969: p. 84, fig. 110. Occasional in bays from Aransas Bay to the lower Laguna Madre, in seagrass and algae beds at salinities from 17 to 36 ppt. Remarks: This subspecies is known only from Texas. Schultz and McCloskey (1967) suggested that the western Atlantic species of *Erichsonella* may represent one or more clines.

*Synidotea* sp. Figure 5. An apparently undescribed species, occasional in the shallow surf of wave-exposed sandy beaches on the upper Texas coast from Sea Rim State Park to High Island.

## SUBORDER ANTHURIDEA
## Family Anthuridae

*Anthelura* sp. Figure 13. An apparently undescribed species, occasional on a sandy-silt substrate at Buccaneer Oil Field spoil area offshore from Galveston at 18.5 m depth.

*Horoloanthura irpex* Menzies and Frankenberg, 1966. Figure 12. Menzies and Frankenberg, 1966: p. 42, fig. 18. Two specimens from offshore on sandy-clay substrate at 47 m depth (UTMSI).

*Xenanthura brevitelson* Barnard, 1925. Figure 11. Menzies and Frankenberg, 1966: p. 38, fig. 15. Several specimens from low energy sandy bays from Galveston Bay to the lower Laguna Madre; also offshore on sandy substrate at 15 m depth (UTMSI). Remarks: Previously known from Georgia, Florida and West Indies at 19 to 137 m depth.

## SUBORDER FLABELLIFERA
## Family Sphaeromatidae

*Ancinus depressus* (Say, 1818). Figure 14. Menzies and Frankenberg, 1966: p. 43, fig. 19. Widely distributed in the bar-trough system of surf-exposed sandy beaches from Sea Rim State Park to South Padre Island.

*Cassidinidea ovalis* (Say, 1818). Figure 15. Menzies and Frankenberg, 1966: p. 44, fig. 20. Several specimens from Aransas Bay, Copano Bay, and Sabine Lake, often associated with oyster reefs, at salinities from 7 to 18 ppt. Remarks: This is an obligate brackish water species, which has been reported in southeast Texas from a freshwater canal (Cover and Harrel 1978) and the lower Neches River (Harrel *et al.* 1976). Schultz (1978) regarded *C. lunifrons* (Richardson) as conspecific with *C. ovalis*.

*Cymodoce faxoni* Richardson, 1905). Figure 18. Menzies and Miller, 1955: p. 292–296. This was the most abundant isopod found in seagrass and algal beds along the southern Texas coast, from Baffin Bay to the lower Laguna Madre, at salinities from 7 to 36 ppt.

*Dynamenella dianae* (Menzies, 1962). Figure 20. Menzies and Glynn, 1968: p. 63, fig. 23, A, B. This was the most abundant isopod on the rock jetties from Matagorda Bay to South Padre Island, at salinities from 23 to 37 ppt. Remarks: This species on the southern Texas coast jetties seems to replace *Sphaeroma quadridentatum*, the most abundant isopod on the northern Texas jetties.

*Exosphaeroma productatelson* Menzies and Glynn, 1968. Figure 19. Menzies and Glynn, 1968: p. 67–68, fig. 33, A–J. Forty-one specimens were collected from a tree branch in the swash zone on the sandy beach at northern Padre Island. The species was originally described from a rocky shore in Puerto Rico, and apparently has not been reported since; the present record may be an accidental stranding. Remarks: The males differ from the original description in that the appendix masculina does not reach the apex of the endopod.

*Sphaeroma quadridentatum* Say, 1818. Figure 16. Schultz, 1978: p. 1–8, figs. 1–3. This was the most abundant isopod on the northern Texas coast, widely distributed on jetties, pilings, submerged wood, and almost any hard substrate, at salinities from 19 to 32 ppt. It was somewhat less abundant on the southern Texas coast, where it was replaced on the jetties and rocks by *Dynamenella dianae*. Remarks: The species was recently redescribed by Schultz (1978), who pointed out sexually dimorphic differences: small tubercles are present on the dorsum of the peraeon and pleotelson of males.

*Sphaeroma walkeri* Stebbing, 1905. Figure 17. Menzies and Glynn, 1968: p. 56, fig. 23,C. We found this species only on the jetty and rocks at South Padre Island, at salinities from 26 to 37 ppt. Remarks: The species has a spotty pantropical distribution and has been found on ship bottoms, suggesting dispersal by that means (Miller 1968). Previously known from Florida, West Indies and Brazil in this hemisphere.

*Limnoria (Limnoria) tripunctata* Menzies, 1951. Figure 21. Menzies, 1957: p. 137–139, fig. 16. Specimens were found in wooden pilings at South Padre Island, on a plank washed up near the south jetty at Port Aransas, and offshore (UTMSI) (probably an accidental occurrence, since the species is a wood-borer).

## Family Cymothoidae

*Aegathoa medialis* Richardson, 1900. Figure 22. Schultz, 1969: p. 149, fig. 221. One specimen (TL 10.8 mm) from the intake screen of the Barney Davis power plant, upper Laguna Madre at Corpus Christi. Remarks: Known previously from Chesapeake and Delaware Bays; reported from a variety of host fishes in the latter region at salinities from 0 to 30 ppt by Watling *et al.* (1974), who suggested that the species might be the juvenile stage of *Livoneca ovalis* (Say).

*Aegathoa oculata* (Say, 1818). Figure 23. Menzies and Frankenberg, 1966: p. 27, fig. 8. This is a common fish ectoparasite, found on *Mugil cephalus* and *Lepisosteus* sp.; it occurred also in net samples from the upper Texas coast and on the intake screen of the Barney Davis power plant. Remarks: The species has been reported as parasitic on *Loligo pealii* (Richardson 1905) and *Bairdiella chrysura* (Menzies and Frankenberg 1966).

*Anilocra laticauda* Milne-Edwards, 1840. Not figured. Menzies and Glynn, 1968: p. 46, fig. 20, A–D. No specimens were collected or examined. The species was reported from Texas by Pearse (1952) as parasitizing *Prionotus tribulus, Sardinella anchovia,* and *Sciaenops ocellatus.*

*Cymothoa oestrum* (Linnaeus, 1758). Not figured. Schultz, 1969: p. 161, fig. 243. No specimens were collected or examined. The species was reported from Texas by Pearse (1952) as parasitizing *Bagre marina* and *Tarpon atlanticus.*

*Livoneca texana* Pearse, 1952. Figure 26. Pearse, 1952: p. 39–40, fig. 150–157. Several specimens parasitic on *Synodus foetens,* about 3 km offshore from Port Aransas. Remarks: The species is known only from Texas; reported by Pearse (1952) from *Synodus foetens, Centropristes philadelphicus* and *Bagre marina.*

*Nerocila acuminata* Schioedte and Meinert, 1881-1883. Figure 25. Richardson, 1905: p. 220–221, fig. 222–223. One specimen parasitic on *Arius felis,* collected near High Island. Remarks: The species has been reported from a variety of host fishes by Richardson (1905) and Pearse (1952).

*Olencira praegustator* (Latrobe, 1802). Figure 24. Menzies and Frankenberg, 1966: p. 30, fig. 11. One specimen (TL 35.5 mm) from a tide trap net collection at UTMSI, Port Aransas. Remarks: This ectoparasite appears to be host-specific in the mouth of species of *Brevoortia* (Watling *et al.* 1974).

*Cirolana mayana* Ives, 1891. Figure 30. Menzies and Glynn, 1968: p. 39, fig. 15, A–D. Six specimens from offshore rocks, banks and reefs: Southern Bank at 60–64 m (UTMSI and TAMU), Hospital Rock at 60 m (TAMU), South Baker Bank at 64 m (TAMU), and West Flower Gardens at 24 m (TAMU). Remarks: The species has been known previously from Puerto Rico, Yucatan, San Francisco and Baja California.

*Cirolana parva* Hansen, 1890. Figure 29. Menzies and Glynn, 1968: p. 38–39, fig. 14, C–D. Several specimens from offshore rocks, banks and reefs: Southern Bank at 64 m (UTMSI), East Flower Gardens at 16 m (TAMU), and Unnamed Bank at 68 m (TAMU). Remarks: The range is extended westward from Mississippi to the offshore Texas coast. This was reported to be the most abundant species on rocky shores and coral in both shallow and deeper water at Puerto Rico (Menzies and Glynn 1968).

*Eurydice littoralis* (Moore, 1902). Figure 28. Menzies and Frankenberg, 1966: p. 49, fig. 24. One specimen (TL 6.0 mm) from the West Flower Gardens on a sand bottom at 24 m (TAMU). Remarks: The species is planktonic as well as benthic (Menzies and Frankenberg 1966).

## Family Excorallanidae

*Excorallana antillensis* (Hansen, 1890). Figure 27. Richardson, 1905: p. 148–149, fig. 131–132. One specimen (TL 17.9 mm) from a rock on Southern Bank at 64 m (UTMSI). Remarks: Apparently a tropical species, known previously from Florida to Puerto Rico.

# SUBORDER GNATHIOIDEA

## Family Gnathiidae

*Gnathia* sp. Figure 10. Two males and two females from 98 m depth offshore on a silty clay substrate (UTMSI). Remarks: This appears to be an undescribed species, which closely resembles *G. crenulatifrons* Monod from the Pacific. The specimens are being described by Richard Kalke (UTMSI).

## SUBORDER ASELLOTA
## Family Stenetriidae

*Stenetrium occidentale* Hansen, 1905. Figure 35. Menzies and Glynn, 1968: p. 71–72, fig. 34 A–E, 35 A–F, 36 D. Several specimens from offshore banks and reefs: 28-Fathom Bank at 52 m (TAMU), Southern Bank at 62 m (TAMU), and West Flower Gardens at 24 m (TAMU). Remarks: This is apparently a tropical species, known previously from Bermuda, Puerto Rico and the West Indies.

## Family Janiridae

*Janira minuta* Richardson, 1902. Figure 36. Schultz, 1969: p. 258, fig. 405. This species is associated with pelagic *Sargassum*, and was collected from *Sargassum* washed up on beaches. Remarks: Menzies and Glynn (1968) believed this species to be conspecific with *Bagatus bermudensis* (Richardson), based on female types of *J. minuta*. The males which we examined do not conform to the description of *B. bermudensis* in that the first male pleopod has the distolateral margins projecting distally beyond the median portion, whereas *B. bermudensis* has the first pleopod apex with a swollen medially recurved tip.

*Jaeropsis* sp. A. Figure 37. One female (TL 2.5 mm) from Hospital Rock on a predominantly clay bottom at 60 m depth (TAMU). This appears to be an undescribed species that closely resembles *J. coralicola* Schultz and McCloskey and *J. dubia* Menzies. Additional material is needed in order to adequately describe the species.

*Jaeropsis* sp. B. Figure 38. One female (TL 2.1 mm) from the Brazos-Santiago jetty at South Padre Island. This specimen resembles *J. lobata* Richardson from the Pacific, but the description of the latter is not well defined (Schultz 1969) and additional material is needed along with a redescription of *J. lobata* to determine if the specimen represents a new species or a range extension for *J. lobata*. It differs from *Jaeropsis* sp. A in having a rounded rather than indented frontal margin and entire rather than serrated lateral pleotelson margins.

## Family Munnidae

*Munna (Uromunna) hayesi* Robertson, 1978. Figure 34. Robertson, 1978: p. 39–46. A few specimens were collected offshore at 15 m depth on a predominantly sand bottom (UTMSI) and from the Buccaneer Oil Field spoil area off Galveston (TAMU). Remarks: The species is known only from Texas; the type locality is the south jetty at Port Aransas.

*Munna (Uromunna) reynoldsi* Frankenberg and Menzies, 1966. Figure 33. Frankenberg and Menzies, 1966: p. 200–208. Several specimens were collected among plant detritus along the upper Texas coast in a brackish coastal marsh, and in a brackish marsh lake in Sea Rim State Park, at salinities from 0 to 4.4 ppt (Callahan *et al.* 1977). Remarks: This is an obligate brackish water species.

## SUBORDER ONISCOIDEA
## Family Ligydidae

*Ligia exotica* Roux, 1828. Figure 31. Richardson, 1905: p. 676–677, fig. 716–718. Abundant and widely distributed on rock jetties, seawalls and pilings along the entire Texas coast. Remarks: This is an amphibious species, found usually above the waterline, although it may escape into the water when disturbed.

## RESULTS AND DISCUSSION

Thirty free-living and seven ectoparasitic species are recorded here from Texas waters. Indicative of our inadequate knowledge of the isopod fauna of the northern Gulf of Mexico is the fact that four (possibly five) of these are apparently undescribed and 15 represent range extensions to Texas. Three of the described species are known only from Texas, indicating little endemism. We found two ectoparasitic species (*Aegathoa medialis* and *A. oculata*) not recorded by Pearse (1952), but two others (*Anilocra laticauda*

and *Cymothoa oestrum*) reported by Pearse were not encountered in this study. Of the ectoparasites, only *Olencira praegustator* seems to be host-specific (Watling *et al.* 1974).

Approximately 50 percent of the species were collected at inshore habitats only, 25 percent occurred only offshore at depths from 3.5 to 98 m, and the remaining 25 percent were recorded both inshore and offshore. Of the free-living species, 14 were identified from offshore material.

Habitat associations of the Texas species are summarized in Table 2. It should be noted that seven species were represented by only one or two individuals. No offshore species was represented by large numbers of individuals and relatively few of the inshore species were sufficiently abundant to be of much quantitative importance in community structure. The numerically most abundant species include *Sphaeroma quadridentatum* on northern coast jetties, rocks, and wooden structures, *Dynamenella dianae* on southern coast jetties and rocks, *Cymodoce faxoni* in algal and seagrass beds, and the ubiquitous *Ligia exotica* on hard intertidal substrates. Rarely were more than three species found in a single collection at any given habitat. The most frequently co-occurring species were *Cymodoce faxoni* and *Erichsonella attenuata* among algal and seagrass beds, and *Dynamenella dianae* and *Sphaeroma walkeri* on jetties and rocks at South Padre Island. The species collected over the widest salinity ranges were *Edotea montosa* (0–26 ppt), *Cymodoce faxoni* (7–36 ppt), *Erichsonella attenuata* (7–35 ppt), and *E. filiformis* (17–36 ppt). *Cassidinidea ovalis* (7–18 ppt, also reported from freshwater) and *Munna reynoldsi* (0–4.4 ppt) are obligate brackish water species.

Geographical affinities of the Texas isopod fauna are summarized in Table 3. The Texas coast is generally considered part of the disjunct temperate

TABLE 3

Geographical Affinities of the Texas Isopod Fauna.

| | Percent affinity |
|---|---|
| North Atlantic coastal, south of Cape Hatteras | 43 |
| North Atlantic coastal, north of Cape Hatteras | 35 |
| North Atlantic coastal and tropical Caribbean | 27 |
| Tropical only | 16 |
| North and South Atlantic coastal | 14 |
| Pacific-Atlantic | 11 |
| Pantropical (known or suspected) | 5 |
| South Atlantic coastal only | 0 |

Carolinian zoogeographical province (Briggs 1974), although the southern extremity of the coast may be regarded as transitional between warm temperate and tropical (Andrews 1977). The Texas isopod fauna predictably shows its greatest relationship to the North Atlantic coast, with a lesser affinity to the tropical Gulf and Caribbean. Fifteen (43 percent) of the 35 species listed from Georgia by Schultz (1978) are recorded here from Texas. Most isopods are obligatory benthonts capable of little if any swimming; furthermore, isopods develop directly from the parental brood pouch and have no planktonic or migratory larval stage. On the other hand, adults of some species may be dispersed as members of fouling communities associated with ships and flotsam, or with the host fish in the case of ectoparasites. Six of the Texas species appear to have more or less strictly tropical distributions. Most of these inhabit shallow sites in the Caribbean, whereas they occurred only at deeper offshore Texas sites, including the Flower Gardens coral reefs. These reefs, located on the outer edge of the continental shelf 203 km SSE of Galveston, are the northernmost coral reefs in the Gulf of Mexico. Depth across most of the reef is 21 to 26 m and water temperatures remain between 21 to 22 C year-round (Cannon and Alexander 1977). The Loop Current may be an important physical factor in the distribution of isopods on the deep reefs and banks off the Texas coast.

Although the total number of recorded Texas species corresponds closely to that known from the Georgia coast, the present study is probably far from complete. For example, Richardson (1905) recorded 106 species known then between Chesapeake Bay and the Caribbean (see Menzies and Frankenberg 1966). Many of these might be expected to occur in Texas, but of that total we recorded only 17. More extensive offshore sampling in particular should be expected to reveal additional species. We hope that our survey may provide an impetus for other workers to add to knowledge of northern Gulf isopods.

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## LITERATURE CITED

ANDREWS, J. 1977. *Shells and shores of Texas.* University of Texas Press, Austin.

BREUER, J. P. 1962. An ecological survey of the lower Laguna Madre of Texas, 1953–1959. *Publications of the Institute of Marine Science, University of Texas.* 8:153–183.

BRIGGS, J. C. 1974. *Marine zoogeography.* McGraw-Hill Book Co., New York.

CALLAHAN, B. J., S. T. CLARK and P. B. ROBERTSON. 1977. Occurrence of the brackish water asellote isopod *Munna (Uromunna) reynoldsi* in Texas. *Gulf Research Reports.* 6(1):77–78.

CANNON, M. S. and E. S. ALEXANDER. 1977. The Flower Garderns coral reefs. *Texas Journal of Science.* 28(1–4):99–102.

COVER, E. C. and R. C. HARREL. 1978. Sequences of colonization, diversity, biomass, and productivity of macroinvertebrates on artificial substrates in a freshwater canal. *Hydrobiologia.* 59:81–95.

DUPLECHIN, J. and B. J. CALLAHAN. 1975. A key to the terrestrial, freshwater, and marine isopods of southeast Texas. (Unpublished report, Biology Department, Lamar University, Beaumont, Texas).

FRANKENBERG, D. and R. J. MENZIES. 1966. A new species of asellote marine isopods, *Munna (Uromunna) reynoldsi* (Crustacea: Isopoda). *Bulletin of Marine Science.* **16**(2):200–208.

GILLESPIE, M. C. 1969. The polyhaline Isopoda of the western Mississippi River delta. *Proceedings of the Louisiana Academy of Science.* **32**:53–56.

HARPER, D. E., JR. 1974. *Ciridotea excavata* n. sp. (Crustacea: Isopoda) from marine waters of Texas. *Contributions in Marine Science.* **18**:229–239.

HARREL, R. C., J. ASHCRAFT, R. HOWARD and L. PATTERSON. 1976. Stress and community structure of macrobenthos in a Gulf coast riverine estuary. *Contributions in Marine Science.* **20**:69–81.

HEDGPETH, J. W. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. *Publications of the Institute of Marine Science, University of Texas.* **3**(1):107–227.

HOOKS, T. A., K. L. HECK, JR., and R. J. LIVINGSTON. 1976. An inshore marine invertebrate community: structure and habitat associations in the northeastern Gulf of Mexico. *Bulletin of Marine Science.* **26**(1):99–109.

MENZIES, R. J. 1951. A new subspecies of marine isopod from Texas. *Proceedings of the U.S. National Museum.* **101**(3289):575–579.

_____ 1957. The marine borer family Limnoriidae (Crustacea, Isopoda). I. Northern and Central American: systematics, distribution, and ecology. II. Additions to the systematics. *Bulletins of Marine Science Gulf and Caribbean.* **7**(2):101–200.

_____ and D. FRANKENBERG. 1966. *Handbook on the common marine isopod Crustacea of Georgia.* University of Georgia Press, Athens, Georgia.

_____and P. GLYNN. 1968. The common marine isopod Crustacea of Puerto Rico: a handbook for marine biologists. *Studies on the Fauna of Curacao and other Caribbean Islands.* **27**:1–133.

_____ and M. A. MILLER. 1955. Redescription of the marine isopod crustacean *"Exosphaeroma" faxoni* Richardson from Texas. *Bulletin of Marine Science Gulf and Caribbean.* **5**(4):292–296.

MILLER, M. A. 1968. Isopoda and Tanaidacea from buoys in coastal waters of the continental United States, Hawaii, and the Bahamas (Crustacea). *Proceedings of the U.S. National Museum.* **125**(3652):1–53.

PEARSE, A. S. 1952. Parasitic Crustacea from the Texas coast. *Publications of the Institute of Marine Science, University of Texas.* **2**(2):5–42, 157 figs.

RICHARDSON, H. 1905. A monograph on the isopods of North America. *Bulletin of the U.S. National Museum.* No. **54**, 717pp.

ROBERTSON, P. B. 1978. A new species of asellote marine isopod, *Munna (Uromunna) hayesi* (Crustacea: Isopoda) from Texas. *Contributions in Marine Science.* **21**:39–46.

SCHULTZ, G. A. 1969. *How to know the marine isopod crustaceans.* Wm. C. Brown Co. Publ, Dubuque, Iowa.

_____ and L. R. McCLOSKEY. 1967. Isopod crustaceans from the coral *Oculina arbuscula* Verrill. *Journal of the Elisha Mitchell Scientific Society.* **83**:103–113.

_____ 1978. Four marine isopod crustaceans from St. Catherines Island with a list of other species from Georgia. *Georgia Journal of Science.* **36**:1–12.

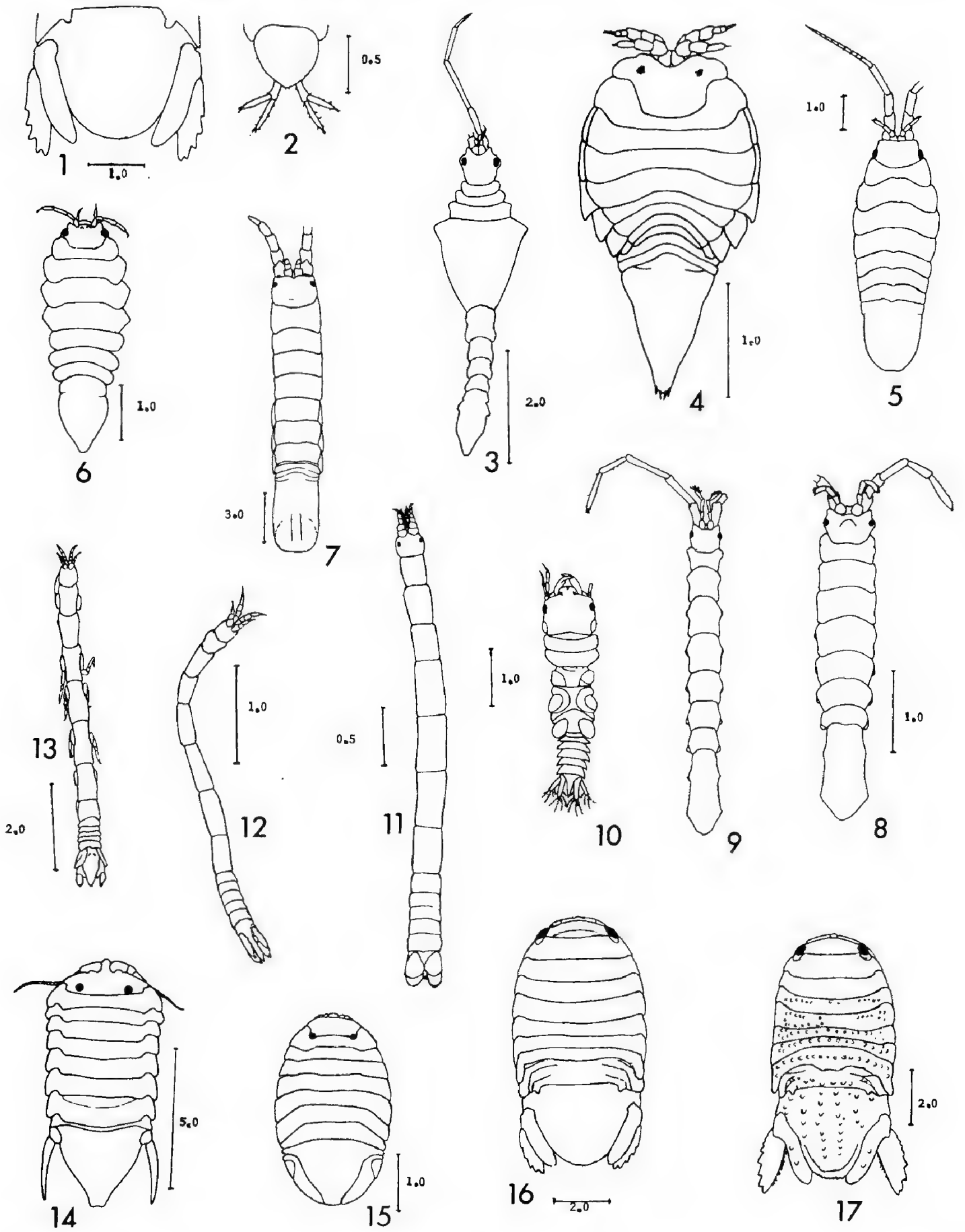
SIMMONS, E. G. 1957. An ecological survey of the upper Laguna Madre of Texas. *Publications of the Institute of Marine Science, University of Texas.* **4**(2):156–200.

WALLACE, N. A. 1919. The isopoda of the Bay of Fundy. *University of Toronto Studies, Biological Series.* No. **18**:1–42.

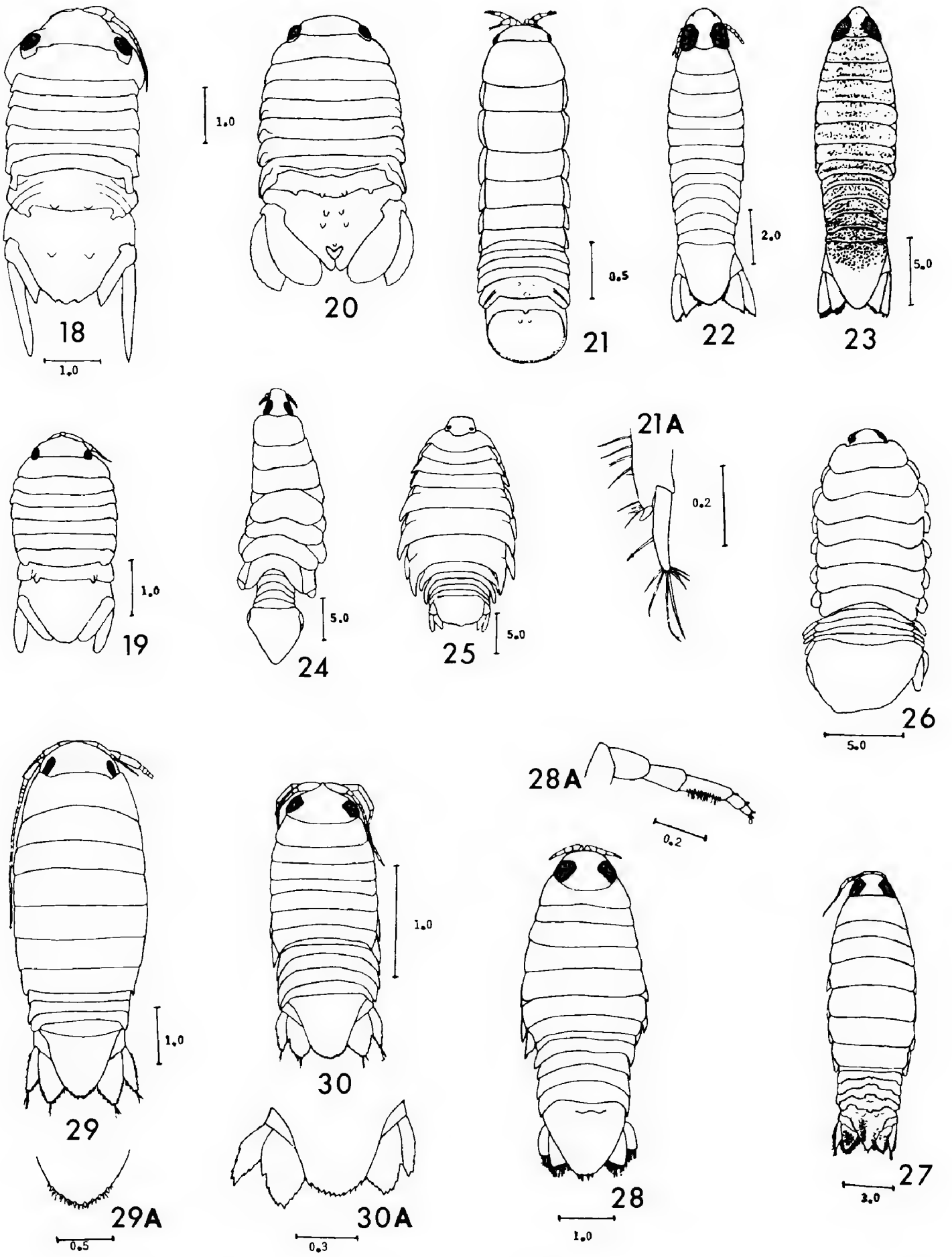
WATLING, L., J. LINDSAY, R. SMITH and D. MAURER. 1974. The distribution of Isopoda in the Delaware Bay region. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie.* **59**(3):343–351.

WHITTEN, H. L., H. F. ROSENE and J. W. HEDGPETH. 1950. The invertebrate fauna of the

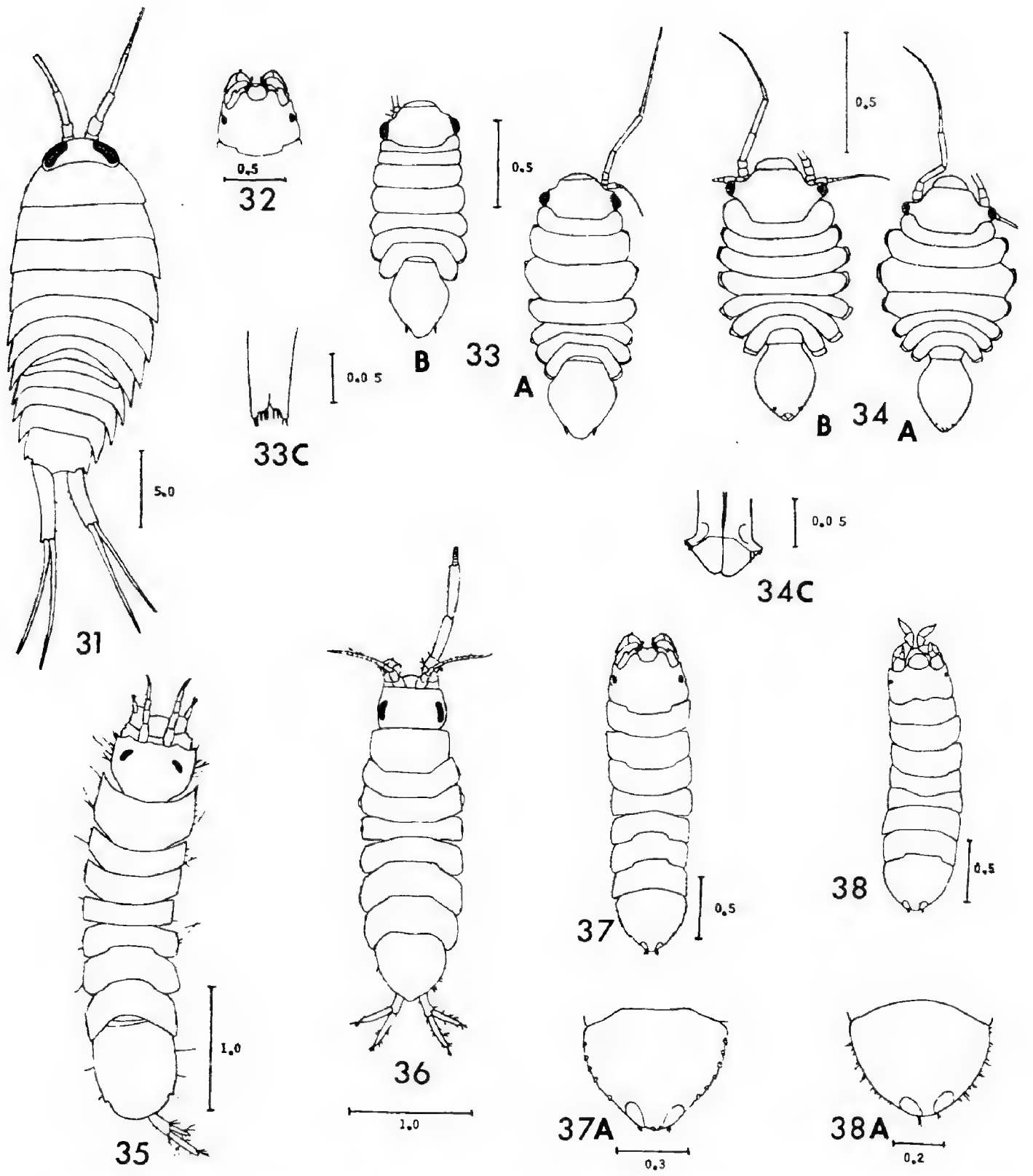
Texas coast jetties; a preliminary survey. *Publications of the Institute of Marine Science, University of Texas.* 1(2):53–86.




FIGS. 1–17. 1, uropods inserted on antero-lateral margin of pleotelson. 2, uropods inserted near posterior margin of pleotelson. 3, *Astacilla lauffi.* 4, *Chiridotea excavata.* 5, *Synidotea* sp. 6, *Edotea montosa.* 7, *Cleantis planicauda.* 8, *Erichsonella filiformis isabelensis* (male). 9, *Erichsonella attenuata* (male). 10, *Gnathia* sp. (male). 11, *Xenanthura brevitelson* (female). 12, *Horoloanthura irpex* (female); 13, *Anthelura* sp. (female). 14, *Ancinus depressus.* 15, *Cassidinidea ovalis.* 16, *Sphaeroma quadridentatum* (female). 17, *Sphaeroma walkeri.*




FIGS. 18–30. 18, *Cymodoce faxoni* (male). 19, *Exosphaeroma productatelson.* 20, *Dynamenella dianae* (male). 21, *Limnoria (Limnoria) tripunctata*; A, uropod. 22, *Aegathoa medialis.* 23, *Aegathoa oculata.* 24, *Olencira praegustator.* 25, *Nerocila acuminata.* 26, *Livoneca texana.* 27, *Excorallana antillensis.* 28, *Eurydice littoralis;* A, antenna 1. 29, *Cirolana parva*; A, pleotelson apex. 30, *Cirolana mayana*; A, pleotelson apex and uropods.




FIGS. 31–38. 31, *Ligia exotica*. 32, Very short antennae 1 and 2 fold against front margin of cephalon. 33, *Munna (Uromunna) reynoldsi*; A, female; B, male; C, distal end of first male pleopods. 34, *Munna (Uromunna) hayesi*; A, female; B, male; C, distal end of first male pleopods. 35, *Stenetrium occidentale*. 36, *Janira minuta*. 37, *Jaeropsis* sp. A.; A, pleotelson. 38, *Jaeropsis* sp. B; A, pleotelson.

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# ABUNDANCE AND DISTRIBUTION PATTERNS OF DEMERSAL FISHES ON THE SOUTH TEXAS OUTER CONTINENTAL SHELF: A STATISTICAL DESCRIPTION[1]

Ronald M. Yoshiyama[2], Joan Holt, Scott Holt, Robert Godbout, and Donald E. Wohlschlag

*University of Texas Marine Science Institute, Port Aransas Marine Laboratory, Port Aransas, Texas 78373*

[1]The University of Texas Marine Science Institute Contribution No. 545

[2]Present Address: Environmental Sciences Division, Oak Ridge National Laboratory, P. O. Box X, Oak Ridge, Tennessee 37830 and Graduate Program in Ecology, University of Tennessee, Knoxville, Tennessee 37916

## ABSTRACT

Results from a three-year trawl survey of benthic fishes, along with supporting data on benthic macroinvertebrates and abiotic parameters, were used in an analysis of temporal and spatial patterns of the benthic ichthyofauna of the south Texas outer continental shelf. The goal was to derive a quantitative description of major patterns and to determine their statistical significance.

Numerical classification indicated general similarity in the ichthyofauna at sampling stations of similar depths, with definite change in character of the ichthyofauna at increasing depths. The degree of similarity among sampling stations, with respect to abundances of fish species, varied between seasons, years, and day/night periods. Groupings of species defined by the numerical classification also varied temporally.

Discriminant analysis was used to determine if groups of sampling stations defined by depth could be differentiated from one another by numerically defined combinations of abiotic and biotic variables. Pronounced separation of station-groups was achieved by discriminant analyses performed separately on selected abiotic variables and on fish and invertebrate abundances. The analyses allowed us to gauge the relative importance of variables contributing to this separation. Among abiotic variables, a combination of mean grain size of the sediment, percent silt composition of the sediment, and bottom salinity were most important in distinguishing among groups. With respect to species, station groups were most clearly differentiated by abundances of (fishes) *Trichopsetta ventralis, Pristipomoides aquilonaris, Cynoscion nothus, Sphoeroides parvus, Syacium gunteri,* and (invertebrates) *Squilla empusa, Penaeus duorarum, Trachypenaeus constrictus, Penaeus setiferus,* and *Penaeus aztecus.*

Multiple regressions were performed to determine the statistical dependence of fish abundances on selected abiotic and biotic variables. The

regressions explained 8 to 57% of the variation in fish abundances, and they were effective for only 9 of the 27 species examined (30–57% of variation explained). These regressions may indicate possible causative relationships between the abundances of fishes and environmental variables, but they must be interpreted with caution in the absence of detailed ecological information on the species.

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## INTRODUCTION

Patterns of distribution and abundance of outer continental shelf fishes off the Texas coast have been examined by a number of workers (*e.g.*, Hildebrand 1954, Chittenden and McEachran 1976; Chittenden and Moore 1977), but ecological aspects of this ichthyofauna, particularly regarding factors which affect these patterns, remain poorly understood. Although distributions of certain species off Texas and in other parts of the Gulf of Mexico have been related in a broad manner to a few obvious factors such as depth, sediment, and temperature (Dawson 1964, Chittenden and McEachran 1976, Lewis and Yerger 1976), a more detailed and quantitative exposition of the relationship between fish populations and the ecological factors which affect them is desirable. The need for statistical evaluations of these fish-environment relationships has been specifically pointed out (Chittenden and Moore 1977).

A multifaceted environmental survey of the south Texas outer continental shelf conducted from 1974 to 1977 (Parker 1976, Groover 1977, Flint and Griffin 1979) has generated a substantial amount of information appropriate for quantitative evaluation of relationships between biotic and abiotic components of this ecosystem. The survey was intended to provide a "baseline" set of data for the south Texas shelf which would serve as an ecological description of the area prior to extensive exploration and development of petroleum resources there. Because it is descriptive in nature, the information obtained represents only a starting point for an investigation of the structure and dynamics of the system. It is a necessary step in that it provides a reference against which results of later studies may be compared. This paper draws from the survey data to describe broadly the demersal ichthyofauna of the region, and it integrates data on benthic epifauna (fishes and invertebrates) and environmental factors to identify possible significant relationships between certain species and features of their environment.

## MATERIALS AND METHODS

The study area spanned approximately 19,250 km$^2$ in the northwestern Gulf of Mexico along the south Texas coast. It was bounded by 96°W longitude on the east, the Matagorda Bay complex on the north, and by the Mexico-United States international border on the south (Flint and Rabalais 1980).

The data consisted of abundances of fishes and macroinvertebrates caught in bottom trawls and measurements of various physical variables for fixed sampling stations (Fig. 1) at regular (seasonal or monthly) time periods. Data on fishes and macroinvertebrate epifauna were

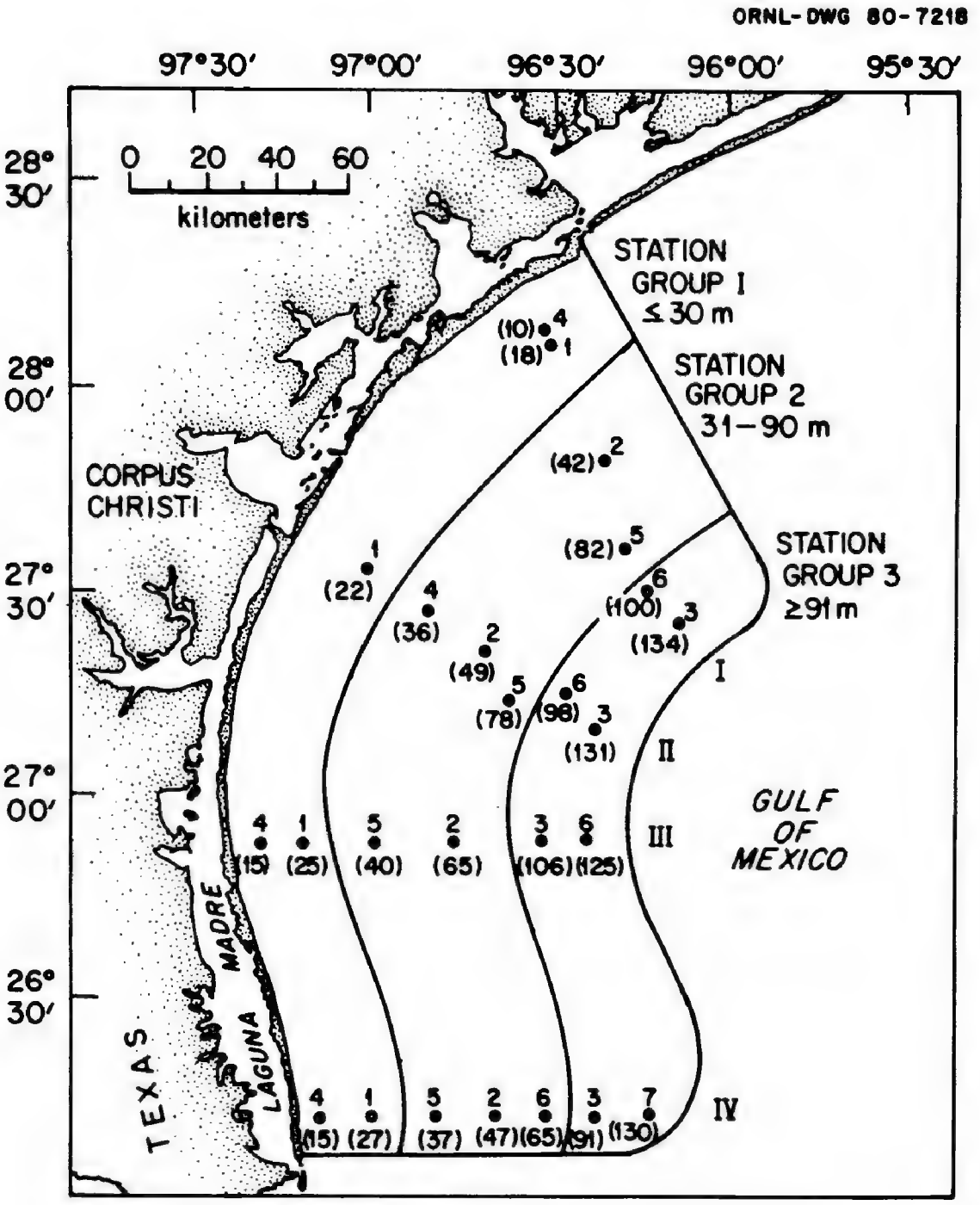



FIG. 1. Sampling stations and defined station-groups, with depth (m) in parentheses. Roman numerals I–IV identify transects.

derived from 15-minute (bottom time) drags with a conventional 10.7-m Gulf coast flat trawl that utilized a 12.2-m lead line and 9.1-m head line. There was a 0.9-m separation between the net wings and the 0.76- by 1.52-m doors (otter boards). Wings and the main body of the net were 44.5-mm stretched mesh of No. 18 nylon twine, and the 3.0-m bag was 25.0-mm stretched mesh of No. 36 nylon twine. A cod-end bag liner of 4.8-mm stretched mesh also was employed during the initial (winter) phase of the first sampling year, but use of the liner had to be discontinued because it caused excessive fouling of the gear with mud and loss of nets. Samples were taken from the *R/V Longhorn* at a dragging speed of approximately two knots. Additional specifics on sampling gear and protocol are given in Wohlschlag (1976). Sampling of invertebrate infauna was carried out with a Smith-MacIntyre bottom sampler of approximately 0.025 $m^3$ capacity. Details on collecting and processing of samples are described in Holland (1977). Methods of collection of hydrographic and geological data are given in Parker (1976), Groover (1977), and Flint and Griffin (1979).

Sampling was from December 1974 through 1977. A total of 569 trawls for fishes and invertebrates was made, with one to three trawls taken during a given sampling episode

(defined as all trawls taken at a single station during a given time period). Sampling effort varied between years (258 trawls in 1977, 239 in 1976, and 72 in 1974–1975) and stations were not all sampled at equal frequencies. However, sampling effort within each year was distributed over all four transects and major depth zones. Trawls were made over the entire range of the sampling area during winter, spring, and fall of each year, with additional trawls (limited to Transect II) taken monthly in 1976 and 1977. A schedule of cruises is given in Wohlschlag (1979).

Sampling stations were divided among three station-groups by depth for summarization and analytical purposes (Fig. 1). The depths dividing station-groups 1 and 2 (30 m) corresponded roughly with the boundary between the white (shallow) and brown shrimp grounds (Chittenden and Moore 1977). The boundary between station-groups 2 and 3 (90 m) was arbitrarily chosen, but it was convenient because it divided the groups such that some degree of parity in sampling effort was achieved (Table 1). These station-groups were employed in discriminant analysis and comparisons of group means (described below).

TABLE 1

Sampling effort over the defined station-groups (Figure 1) during 1974–1977.[1]

| Year | Number of trawls | | |
|---|---|---|---|
| | Station-group 1 | Station-group 2 | Station-group 3 |
| 1974-1975 | 24 | 24 | 24 |
| 1976 | 66 | 104 | 69 |
| 1977 | 69 | 105 | 84 |

[1]Sampling was initiated in December of 1974.

Our analysis of data consisted of: (1) cluster analysis, to determine overall patterns of distribution and abundance of benthic fishes; (2) discriminant analysis and comparisons of means and variances on data for abiotic variables and on invertebrate epifauna and benthic fish abundances, to provide further description of spatial trends; and (3) finally, multiple regressions of abundances of the most common fishes against selected abiotic factors and abundance/diversity indices for the invertebrate fauna, to describe quantitatively the association between fish abundances and predictor variables.

## Cluster Analysis

Cluster analysis was performed with a modified version of computer programs developed by Dr. R. W. Smith of the University of Southern California and Anderberg (1972) and used by Holland (1977) and Wohlschlag (1977). We employed the Canberra-Metric (*C.M.*) measure (Lance and Williams 1967a) to represent the dissimilarity between two entities (entities being either individual species or sampling stations or clusters thereof):

$$C.M._{jk} = \frac{1}{n} \sum_{i}^{n} \frac{|X_{ij} - X_{ik}|}{(X_{ij} + X_{ik})} \quad ,$$

where $n$ is the number of attributes considered in measuring similarity and $X_{ij}$ and $X_{ik}$ are the values of attributes $X_i$ for entities $j$ and $k$, respectively.

We used the "flexible clustering" strategy of Lance and Williams (1967b), with the constraint parameter $\beta$ set at $-0.25$ by the convention of other workers (Clifford and Stephenson 1975). Cluster analysis was performed in both normal and inverse modes to provide groupings of sampling stations and groupings of species, respectively.

We applied cluster analysis separately to data for demersal fishes for each season (winter, spring, fall) within each of the years 1976 and 1977. (We did not utilize data from 1974–1975 for cluster analysis because of the insufficient number of samples taken and also because discontinuation in the use of a net liner for sampling during that period may have biased the data.) Separate analyses also were done for day and night periods within each season, so a total of 12 cluster analyses was performed.

## Discriminant Analysis and Comparison of Station-Group Means

Discriminant analysis was applied to selected abiotic variables: (1) to determine if the defined station-groups (Fig. 1) could be distinguished from one another on the basis of abiotic characteristics and (2) to identify those abiotic variables which appeared most important in differentiating the station-groups. The abiotic variables were bottom water temperature (°C) and salinity (‰), mean grain size ($\phi$ units) of the sediment, standard deviation and skewness of the sediment grain size distribution ($\phi$) where the term $\phi$ is $\log_2$ of diameter of sediment in milimeters, and percent silt composition of the sediment. The extent to which the first goal was achieved was measured in three ways. We measured directly the distinctiveness of station-groups by use of the squared canonical correlation for each discriminant function and Wilks' Lambda criterion. Each squared canonical correlation was interpreted as the proportion of variance in the corresponding discriminant function accounted for by the groups (Klecka 1975), and Wilks' Lambda was used to test the significance of the overall difference among station-group centroids (Tatsuoka 1971, Klecka 1975). A third, indirect measure of the strength of groups was the proportion of stations correctly assigned to groups by the classification feature of discriminant analysis.

The relative importance of the original ("discriminating") variables in separating station-groups was gauged by the "standardized weights" (standardized discriminant function coefficients) assigned to the variables by the analysis (Tatsuoka 1971).

We also applied discriminant analysis, which utilized, as discriminating variables, the abundances of numerically dominant fishes and (separately) benthic macroinvertebrates, again to demonstrate differences among the defined station-groups and also to identify species that contributed most to these differences.

Discriminant analyses were performed using the Statistical Package for the Social Sciences (SPSS; Nie *et al.* 1975), which included pairwise comparisons of station-group centroids, based on the Mahalonobis distance between groups. As with the overall test of difference using Wilks' Lambda, these comparisons served to test the distinctiveness of the defined station-groups.

Means and variances for each abiotic and abundance variable were tested for equality over station-groups. Values for percent silt in the sediment were first transformed to arcsines to make the data more normally distributed (Sokal and Rohlf 1969). We tested for equality of variances using Bartlett's test (Sokal and Rohlf 1969) and Cochran's $C$ statistic for both untransformed variables and variables transformed by square root and natural log. If homogeneity was improved by transformation, the most effective transformation was carried over into the subsequent test for equality of means.

Variables with homogeneous variances over station-groups were tested for equality of station-group means by Analysis of Variance (ANOVA), followed by *a posteriori* pairwise comparisons (Student-Newman-Keuls procedure; Sokal and Rohlf 1969). If variances were not homogeneous, we employed an approximate test of means (Sokal and Rohlf 1969, p. 372) for abiotic variables and the Kruskal-Wallis test for individual species abundances.

Data from the entire sampling period (1974-1977) were used in discriminant analyses and in comparisons of station-group means and variances. We felt that nonuniformity in sampling due to use of a net liner in taking the earlier samples would have no effect on the results of these analyses because no comparisons between time periods were made.

## Multiple Regression

The final phase of analysis involved multiple regression of abundances of common fishes against the following predictor variables (nontransformed): sampling transect, depth, year, time of day, Julian day, bottom temperature, bottom salinity, percents silt, sand and clay in the sediment, sediment mean grain size, skewness and standard deviation of sediment grain sizes, percent of sediment (by weight) comprised of organic carbon, number of invertebrate epifauna species, invertebrate epifauna abundance (total number of individuals), invertebrate infauna abundance, and Shannon-Wiener diversity index for invertebrate infauna. Data only from 1976 and 1977 were available for predictor variables and so regression analyses pertain to these two years. We employed polynomial regression with up to fourth degree terms, using a forward (inclusion) stepwise procedure with the constraint that all abiotic predictor variables were considered before biological variables for entry into the regression. Preliminary regressions indicated that considering interaction terms did not improve the fit of the regression to the data, and so interaction terms were not included in subsequent regressions.

Regressions were performed using SPSS and were based on the model:

$$Y = B_0 + B_1X_1 + B_2X_1^2 + B_3X_1^3 + B_4X_1^4 + \ldots +$$

$$B_{4p+1}X_p + B_{4p+2}X_p^2 + B_{4p+3}X_p^3 + B_{4p+4}X_p^4 + e_0 \quad ,$$

where $Y$ is predicted abundance, $X_1 \ldots X_p$ are predictor variables, $B_1 \ldots B_{4p+4}$ are partial regression coefficients, $B_0$ is a constant, and $e_0$ an error term assumed to be independently distributed as normal $(0, \sigma^2; \sigma^2$ unknown). The effectiveness of the model was gauged using the squared multiple-$R$ ($R^2$), which represented the proportion of variability in fish abundance explained by each regression (Afifi and Azen 1972, Klecka 1975).

The role of "sampling error" in influencing our results deserves brief mention. Because of the low level of replication (at most 3 trawls per station during a sampling period) employed in the sampling program, our sample estimates of relative fish abundances probably did not accurately reflect the actual abundances at single stations, particularly since many species are known to have patchy distributions (*i.e.*, form schools or loose aggregations; Vetter 1978). To alleviate this problem, we pooled or averaged samples whenever possible, and concentrated on the broader patterns emerging from the analyses. Although our results at the more detailed levels may be far from exact, they should correctly portray the general features of the system.

## RESULTS

Over 160 fish species were captured during the three years of sampling, but only 57 species were captured in excess of 100 individuals and 22 species in excess of 1000. The most abundant and frequently captured fishes (Table 2) included species with pelagic as well as demersal habits (*e.g., Anchoa hepsetus, Trachurus lathami, Peprilus burti*), in addition to strictly benthic forms. Most of the common species were dominant elements (*i.e.*, among the ten most abundant species in a given season) of the ichthyofauna in only one or two station-groups. For example, *Syacium gunteri* and *Diplectrum bivittatum* were predominant in station-groups 1 and 2 and *Serranus atrobranchus* was predominant in station-groups 2 and 3, which reflected the spatial (depth) differences in the fish assemblages found over the study area. The notable exception was *Trachurus lathami*, which was dominant at roughly equal frequencies in all three station-groups. Seasonal changes in the extent to which species dominated the ichthyofauna also occurred (*e.g., Syacium gunteri* predominated mainly in winter and fall), although a number of species showed no variation (*e.g., Stenotomus caprinus, Serranus*

TABLE 2

**Total abundance and number of occurrences (number of trawls in which taken) of the most abundant fishes captured during 1974–1977.[1]**

| Species | No. of individuals | No. of occurrences |
|---|---|---|
| *Trachurus lathami* (Trac) | 8612 | 243 |
| *Serranus atrobranchus* (Ser) | 8406 | 365 |
| *Micropogonias undulatus* (Mic) | 7767 | 140 |
| *Peprilus burti* (Pep) | 6656 | 169 |
| *Cynoscion nothus* (Cyn-n) | 5952 | 123 |
| *Syacium gunteri* (Syac) | 4465 | 263 |
| *Stenotomus caprinus* (Sten) | 3905 | 327 |
| *Pristipomoides aquilonaris* (Prist) | 3534 | 312 |
| *Prionotus paralatus* (Prio-p) | 2608 | 235 |
| *Polydactylus octonemus* (Poly) | 2392 | 65 |
| *Saurida brasiliensis* (Saur) | 2162 | 194 |
| *Anchoa hepsetus* (Anch) | 1987 | 59 |
| *Chloroscombrus chrysurus* (Chlo) | 1945 | 65 |
| *Sphoeroides parvus* (Spho) | 1724 | 163 |
| *Upeneus parvus* (Upe) | 1724 | 217 |
| *Centropristis philadelphica* (Cent) | 1705 | 297 |
| *Prionotus stearnsi* (Prio-st) | 1635 | 187 |
| *Cynoscion arenarius* (Cyn-are) | 1431 | 130 |
| *Prionotus rubio* | 1429 | 217 |
| *Trichopsetta ventralis* | 1390 | 193 |
| *Synodus foetens* | 1186 | 308 |
| *Diplectrum bivittatum* | 1072 | 133 |
| *Porichthys porosissimus* | 957 | 189 |
| *Pontinus longispinis* | 548 | 73 |
| *Synodus poeyi* | 512 | 112 |
| *Bollmannia communis* | 507 | 112 |
| *Lepophidium graellsi* | 455 | 149 |

[1] Abbreviations in parenthesis are used in Table 3.

*atrobranchus*). More extensive descriptions of these patterns are given in Wohlschlag (1977, 1979).

## Cluster Analysis

The major station-clusters as derived from cluster analysis were generally delimited by depth (Fig. 2). Subclusters within major station-clusters also tended to show depth divisions. The indication therefore was that stations of similar depth tended to have fish assemblages of similar composition. However, the demarcation between the major groupings varied from season to season, between years, and between day and night within a season.

Species-clusters as derived from cluster analysis (*e.g.*, Table 3) showed differences between seasons, years, and between day and night with respect to both the number of major groupings obtained and their species composition. Full tables of species-clusters are extensive and cannot be presented here (see Wohlschlag 1977), but the abbreviated Table 3 sufficiently displays cluster patterns for some of the major species. A few species tended to occur

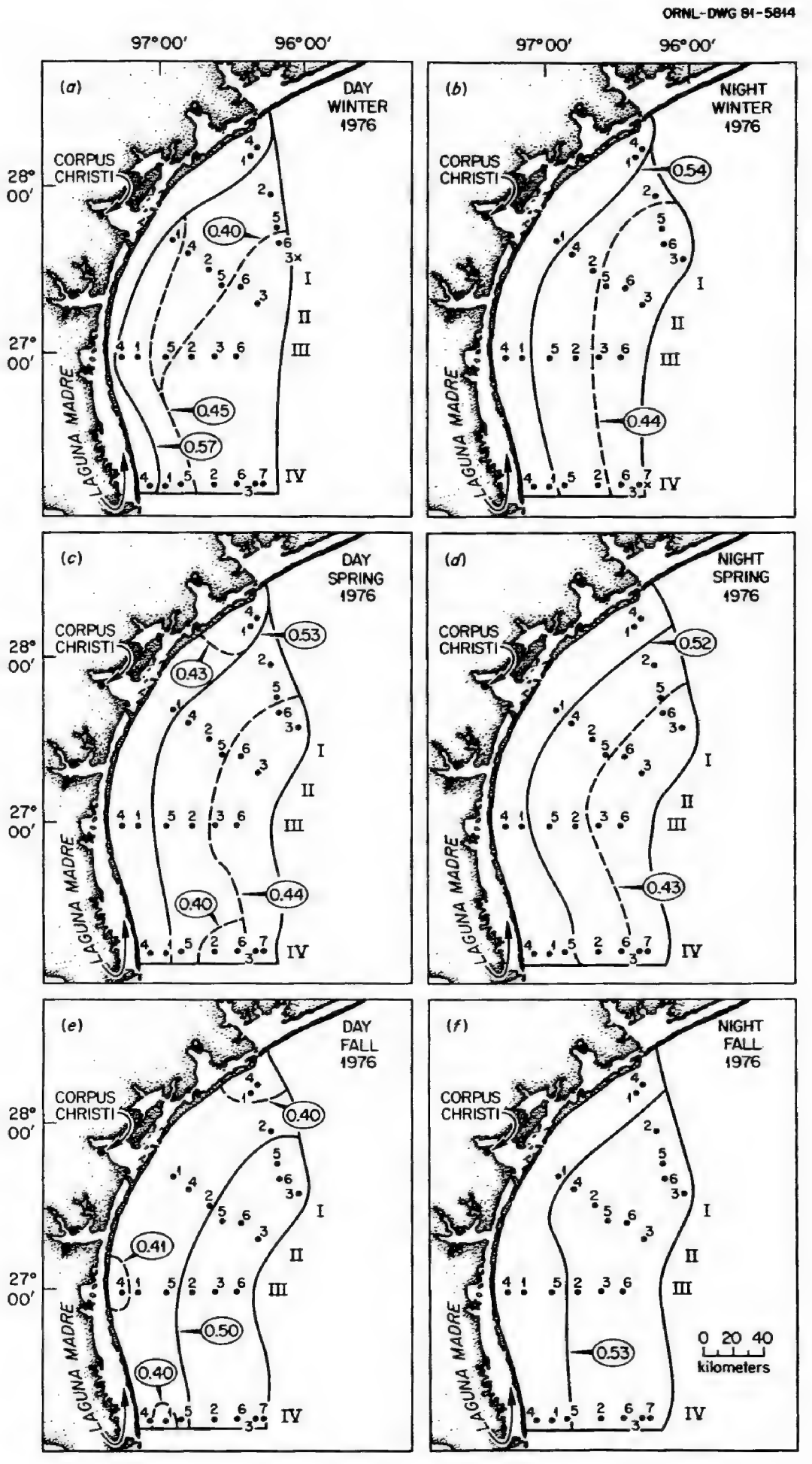
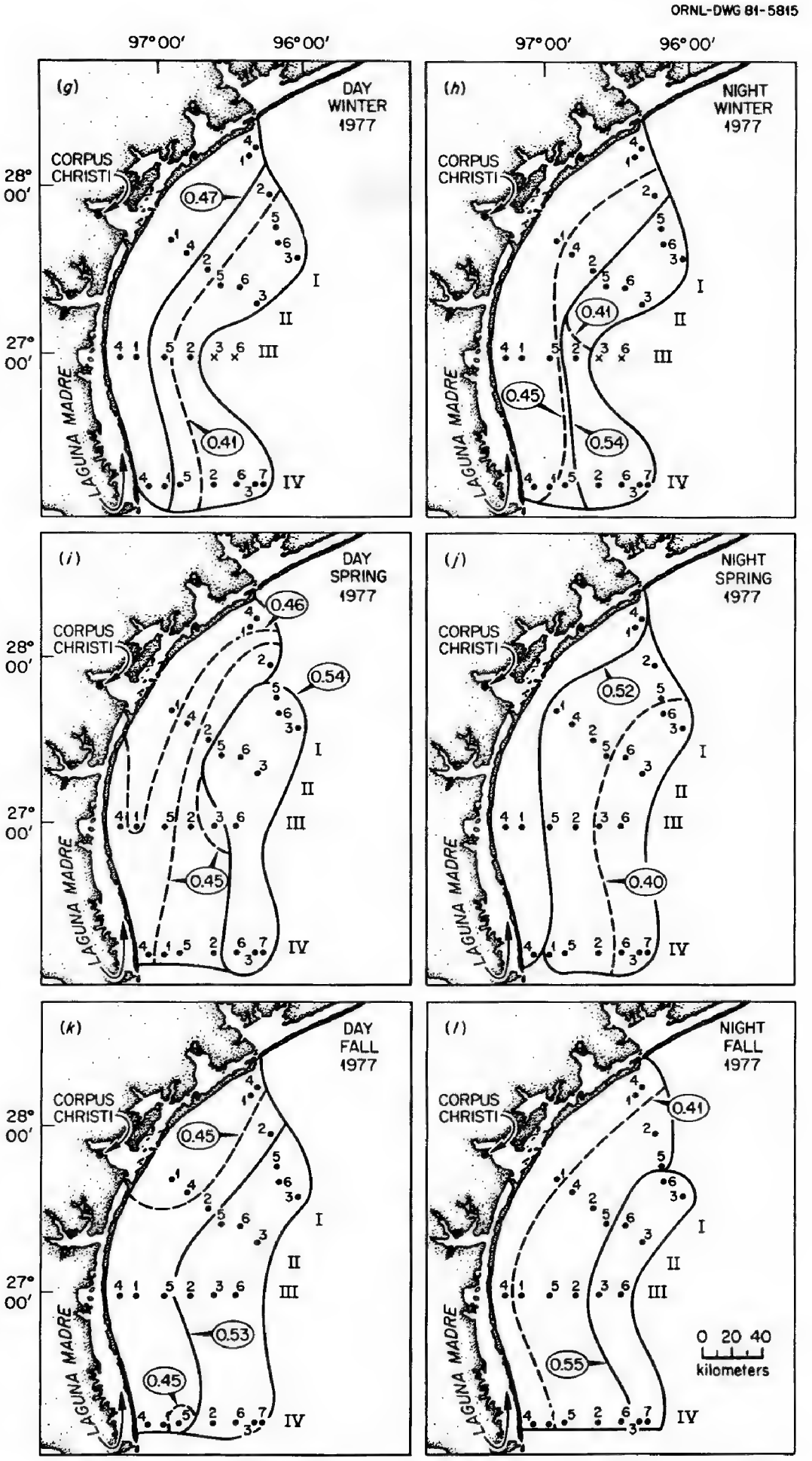



FIG. 2. Major station clusters (solid lines) defined by cluster analysis of fish abundances for (day/night periods in winter, spring, and fall of 1976 and 1977). Dashed lines delineate subclusters within major clusters. Dissimilarity values between clusters are circled. For day-fall




1976 (panel e), stations I-1, I-4, and IV-1 belong to the same subcluster. Symbol x denotes stations that were not sampled during a given time period.

TABLE 3

**Examples of abridged species-groups obtained from six separate cluster analyses for day or night periods in winter, spring, and fall of 1977. Species[1] grouped together belong to the same species-group. Only the 18 most abundant species from Table 2 are listed in these species-groups.**

| Winter 1977 | | | Spring 1977 | | | Fall 1977 | | |
|---|---|---|---|---|---|---|---|---|
| Day | | | Day | | | Day | | |
| Anch | Cyn-are | Cyn-n | Cent | Prio-p | Prist | Spho | | |
| Mic | Pep | Syac | Ser | Sten | Upe | | | |
| | | | | | | Anch | Cent | Chlo |
| Cent | Prio-p | Prio-st | Pep | Trac | | Cyn-are | Cyn-n | Mic |
| Prist | Saur | Ser | | | | Pep | Poly | Saur |
| Spho | Sten | Trac | Anch | Chlo | Cyn-n | Syac | | |
| | | | Mic | Poly | Prio-st | | | |
| | | | Saur | Syac | | Prio-p | Prist | Ser |
| | | | | | | Prist | Sten | Upe |
| | | | | | | Prio-st | | |
| Night | | | Night | | | Night | | |
| Mic | | | Cyn-are | | | Prio-p | Prist | Ser |
| | | | | | | Sten | Trac | Upe |
| Cyn-are | Cyn-n | Pep | Chlo | Cyn-n | Mic | | | |
| Saur | Spho | Syac | Poly | Spho | | Cent | Cyn-are | Cyn-n |
| | | | | | | Mic | Pep | Poly |
| Cent | Prio-p | Prio-st | Pep | Saur | Syac | Prio-st | Spho | Syac |
| Prist | Ser | Sten | | | | | | |
| Upe | | | Cent | Prio-p | Prio-st | Anch | | |
| | | | Prist | Ser | Sten | | | |
| | | | Trac | Upe | | Saur | | |

[1] Full species names corresponding to abbreviations used are given in Table 2.

together (*e.g., Stenotomus caprinus, Pristipomoides aquilonaris,* and *Serranus atrobranchus*; or *Cynoscion nothus, Polydactylus octonemus* and *Micropogonias undulatus*). However, most species showed weaker association with each other, which undoubtedly reflected sampling error and spatially patchy distributions but probably also reflected seasonal fluctuations in abundance and movements of some species between depth zones.

Thus, the major result which emerged from cluster analysis was that temporal variation occurred in assemblages of fishes found in different depth-zones. This variation was reflected by the general lack of consistency in station- and species-clusters between seasons, years and between day and night periods. Moreover, the shifts in boundaries, which separated major station-clusters, indicated that no single station grouping derived from cluster analysis was superior to the station-groups defined in Fig. 1. The lack of superiority of any single station grouping was because none was temporally stable, and therefore provided the justification for the use of the defined grouping scheme in the other analyses.

## Discriminant Analysis and Comparison of Station-Group Means

Discriminant analysis, applied to data on abiotic variables, with groups defined as in Figure 1, produced two discriminant functions. The first function was substantially more important (by roughly four times) than the second in differentiating between station-groups (importance was judged using the discriminant criteria; Table 4). A plot of discriminant scores for data cases (trawl samples) on the discriminant space revealed a reasonably clear separation of station-groups, although some overlap among groups occurred (Fig. 3). The difference among groups was statistically significant as indicated by both Wilks' Lambda (Table 4) and pairwise comparisons (*F*-test) based on the Mahalonobis distance between groups ($p < 0.001$; all comparisons). However, we view these tests (and those for the other discriminant analyses) as only approximate since group covariance matrices could not be assumed equal.

Judging from values for the squared canonical correlation (Table 4), station-groups accounted for 81% of the variation among sampling stations with respect to the first discriminant function and for 56% on the second function. Thus, the influence of the station-groups was substantial. Also, the moderately high proportion (0.81) of correct assignments of stations to groups by the classification phase of the analysis indicated satisfactory discrimination between station-groups.

The most important variables (based on standardized weights) that contributed to the first discriminant function were mean grain size, salinity, and percent silt (Fig. 3). That is, these three variables served most to discriminate between station-groups with respect to the first discriminant function. Mean grain size, skewness, and standard deviation of the grain size distribution served most to separate station-groups on the second discriminant function, but the overall importance of the latter two variables was low because they contributed mainly to the less important second function.

TABLE 4
Results of discriminant analyses based on six abiotic variables and on abundances of the 27 most common benthic fishes and 24 most common epifaunal invertebrate species.

| Variables (No. of data cases[1]) | Discriminant function | Largest discriminant criterion[2] | Proportion of criterion total | Canonical correlation squared | Wilks' Lambda (Chi-square test) |
|---|---|---|---|---|---|
| Abiotic variables | 1 | 1.970 | 0.809 | 0.814 | 0.230 |
| (186) | 2 | 0.467 | 0.191 | 0.564 | ($P << 0.001$) |
| Fishes | 1 | 0.770 | 0.652 | 0.435 | 0.400 |
| (459) | 2 | 0.411 | 0.348 | 0.291 | ($P << 0.001$) |
| Invertebrates | 1 | 0.577 | 0.678 | 0.366 | 0.498 |
| (425) | 2 | 0.274 | 0.322 | 0.215 | ($P << 0.001$) |

[1]Stations at specified time periods.

[2]Equal to the largest eigenvalue obtainable from any linear combination of the abiotic and biotic variables (Tatsuoka 1971).

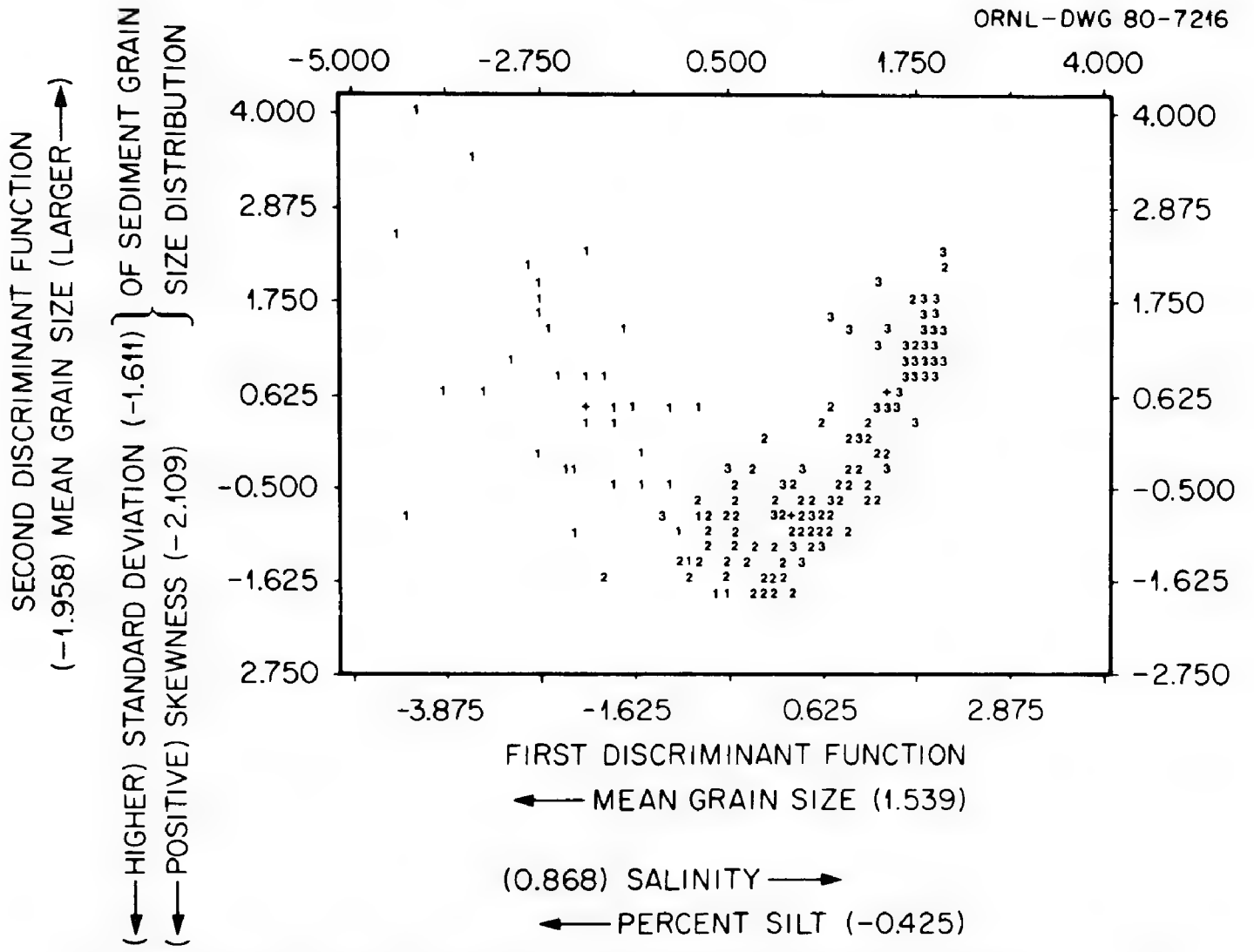



**FIG. 3. Discriminant space based on analysis of abiotic variables. Each number represents a sampling episode (sampling station for a given time period), with value equal to station-group number. Symbol (+) denotes a group centroid. Variables with the greatest (absolute value) standardized discriminant weights (in parentheses) are listed on each axis. Arrows indicate increasing values.**

Discriminant analyses based on fish and macroinvertebrate abundances each yielded two discriminant functions (Table 4). For both analyses, the first discriminant function was roughly twice as important as the second in separating station-groups. The species that were prominent with respect to the discriminant functions (*i.e.*, had standardized weights of greatest magnitudes) are shown for fishes in Fig. 4. Among invertebrates, the most prominent species were in decreasing order of prominence: *Squilla empusa, Penaeus duorarum, Trachypenaeus constrictus, Penaeus setiferus, Penaeus aztecus, Anasimus latus, Solenocera vioscai, Renilla mulleri, Squilla chydaea, Brissopsis alta, Astropecten duplicatus,* and *Acetes americana.* Plots of discriminant scores again showed fairly clear separation of groups (*e.g.*, Fig. 4), with some overlap between groups. Differences among groups were significant (approximate statistics) for both fish and invertebrate data, as indicated by Wilks' Lambda (Table 4) and pairwise comparisons of group centroids based on Mahalonobis distances ($p < 0.001$, all comparisons). Discriminant analysis of fish data therefore corroborated the results of cluster analysis; *i.e.*, there was a depthwise change in the ichthyofauna.

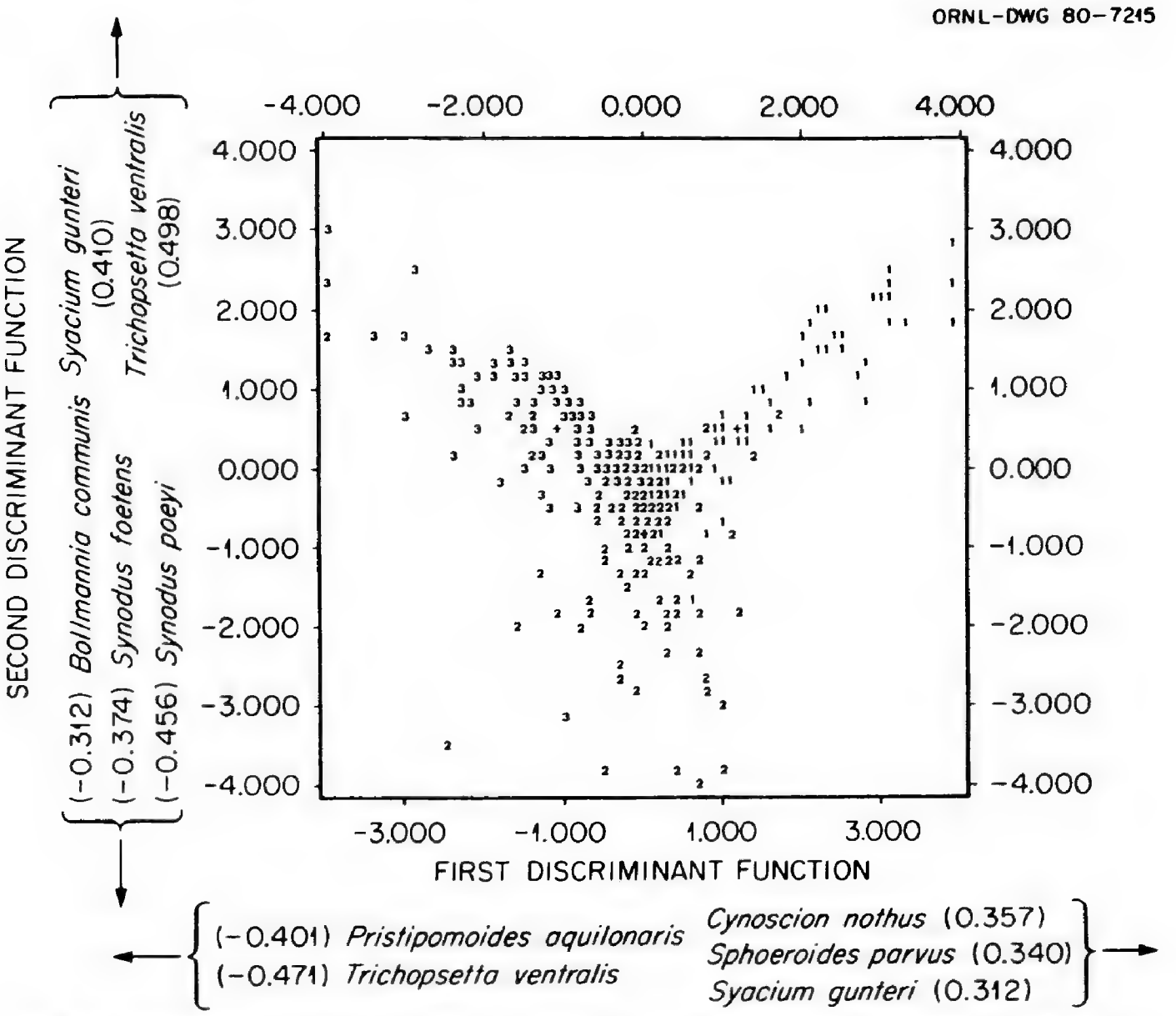



FIG. 4. Discriminant space based on analysis of fish abundances. Format as in Fig. 3.

With respect to fish abundances, station-groups accounted for 44% of the variation among stations on the first discriminant function and for 29% on the second function (Table 4), which indicated that fish abundances were substantially less effective in separating station-groups than were abiotic variables. Values from the analysis of invertebrate abundances were 37% and 22% of the variation explained by groups on the first and second discriminant functions, respectively. Thus, somewhat poorer separation of station-groups was achieved with invertebrate abundances than with fish abundances. The proportion of stations correctly classified into station-groups by discriminant scores for fish and invertebrate abundances were 0.76 and 0.72, respectively. Although lower than the proportion correctly classified by abiotic variables, these values are still high enough to support the definition of station-groups by depth.

Tests for equality of variances among station-groups showed significant heterogeneity for all abiotic variables except standard deviation of grain sizes, which had marginally significant heterogeneity ($p = 0.05$). Results of ANOVA and *a posteriori* comparisons for this variable therefore are considered to be exact. All physical variables showed significant differences

among group means ($p < 0.001$; Table 5). *A posteriori* tests were performed only on standard deviation of grain sizes, which showed individual station-groups to be significantly different from each other ($p \leq 0.05$), since the overall ANOVA was not applicable to the other variables.

TABLE 5

Means (and standard deviations) of abiotic variables for station-groups. Means were tested for equality by ANOVA followed by Student-Newman-Keuls procedure (SNK) if variances were homogeneous over groups, or by an approximate test (Approx.) if variances were nonhomogeneous (Sokal and Rohlf 1969).

| Variable | Group 1 n = 48[1] | Group 2 n = 78 | Group 3 n = 60 | Test of means (significance) |
|---|---|---|---|---|
| Standard deviation of grain sizes[2] | 3.257 (0.481) | 3.421 (0.354) | 3.044 (0.380) | ANOVA ($P$ <<0.001) |
| Temperature (°C) | 22.103 (5.648) | 21.3148 (3.114) | 18.654 (2.175) | Approx. ($P$ < 0.001) |
| Salinity (°/$_{oo}$) | 34.304 (1.672) | 36.003 (0.537) | 36.262 (0.416) | Approx. ($P$ < 0.001) |
| Mean grain size ($\phi$) | 5.895 (1.604) | 7.858 (1.107) | 8.948 (1.165) | Approx. ($P$ < 0.001) |
| Arcsine (% Silt x 100) | 0.242 (1.143) | 0.356 (0.099) | 0.307 (0.059) | Approx. ($P$ < 0.001) |
| ln (Skewness of grain size)[3] | -0.191 (1.054) | -1.041 (1.113) | -0.206 (.501) | Approx. ($P$ < 0.001) |

[1] n is the number of data values.

[2] Each group-mean significantly different from the others (SNK, $P \leq 0.05$).

[3] ln = natural log.

Variances of species abundances were significantly different ($p < 0.05$) among station-groups for all species except the fish *Stenotomus caprinus* and the invertebrates *Amusium papyraceus* and *Parapenaeus longirostris.* Mean species abundances were significantly different over station-groups for most species ($p < 0.05$, ANOVA or $p < 0.025$, Kruskal-Wallis). Only 2 of 27 fishes (*Trachurus lathami* and *Lepophidium graellsi*) and 1 of 24 invertebrates (*Tethyaster vestitus*) showed no difference in mean abundance over station-groups.

To further examine the relationship of species abundances to depth, we employed the Student-Newman-Keuls (SNK) procedure for pairwise comparisons of mean abundance in the three defined station-groups. This was mainly an operational device for grouping together species that showed similar depth-related abundance patterns (Fig. 5) rather than a strict

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| | SPECIES-GROUP | STATION-GROUPS 1 | 2 | 3 |
|---|---|---|---|---|
| 1 | MICROPOGONIAS UNDULATUS | 53.34 | 1.23 | 0.06 |
| | ANCHOA HEPSETUS | 15.32 | 0.09 | 0.01 |
| | POLYDACTYLUS OCTONEMUS | 15.84 | 0.86 | 0.00 |
| | CYNOSCION NOTHUS | 41.62 | 0.51 | 0.01 |
| | CHLOROSCOMBRUS CHRYSURUS | 14.47 | 0.62 | 0.00 |
| | CYNOSCION ARENARIUS | 8.36 | 0.89 | 0.16 |
| | SPHOEROIDES PARVUS | 9.66 | 1.71 | 0.04 |
| | PEPRILUS BURTI | 30.56 | 5.55 | 0.67 |
| | PRIONOTUS RUBIO | 6.19 | 2.34 | 0.79 |
| 2 | BOLLMANNIA COMMUNIS | 0.29 | 1.95 | 0.20 |
| | SAURIDA BRASILIENSIS | 2.73 | 7.91 | 1.45 |
| | SYNODUS POEYI | 0.03 | 2.22 | 0.12 |
| | SYNODUS FOETENS | 2.10 | 3.17 | 1.20 |
| | PRIONOTUS STEARNSI | 0.88 | 6.18 | 1.57 |
| 3 | PRIONOTUS PARALATUS | 0.06 | 2.42 | 10.27 |
| | PONTINUS LONGISPINIS | 0.00 | 0.10 | 3.11 |
| 4 | DIPLECTRUM BIVITTATUM | 2.05 | 2.96 | 0.01 |
| | CENTROPRISTIS PHILADELPHICA | 3.99 | 3.96 | 1.20 |
| 5 | SERRANUS ATROBRANCHUS | 0.34 | 21.18 | 22.58 |
| 6 | SYACIUM GUNTERI | 16.13 | 9.50 | 0.18 |
| | PRISTIPOMOIDES AQUILONARIS | 0.23 | 4.63 | 14.69 |
| | TRICHOPSETTA VENTRALIS | 0.01 | 1.26 | 6.40 |
| 7 | TRACHURUS LATHAMI | 22.95 | 15.89 | 11.94 |
| | LEPOPHIDIUM GRAELLSI | 0.82 | 1.01 | 0.61 |
| | STENOTOMUS CAPRINUS | 5.76 | 6.97 | 7.47 |
| | UPENEUS PARVUS | 2.23 | 3.37 | 4.57 |
| 8 | PORICHTHYS POROSISSIMUS | 0.86 | 2.79 | 1.58 |

FIG. 5. Species-groups of common fishes based on mean abundances per trawl in the three defined station-groups (Fig. 1). Species-groups were determined by applying the Student-Newman-Keuls procedure as an approximate test for similarities. Means enclosed by the same box do not differ significantly ($p > 0.05$). For *Porichthys porosissimus,* means for station-groups 1 and 2 were significantly different, although means were not significantly different between station-groups 1 and 3 and between station-groups 2 and 3.

statistical test because most species had heterogeneous variances for abundances among station-groups, which compromised the accuracy of the SNK procedure. The 27 species were divisible into 7 groups. Most "significant" differences were based on greater mean abundance in one station-group than in the other two (species-groups 1, 2 and 3). Only three species (species-groups 4 and 5) had significantly lower abundance in one station-group than in the other two. Five species (species-group 2) had significantly greater abundance in station-group 2 (mid-shelf) but none had significantly lower abundance there. The abundances of three species (species-group 6) were significantly different for each station-group while four species (species-group 7) showed no differences between station-groups. Other less common fishes not included in Fig. 5 also differed in spatial distribution. In general, species restricted to outer-shelf stations were not as abundant as those restricted to the inner shelf.

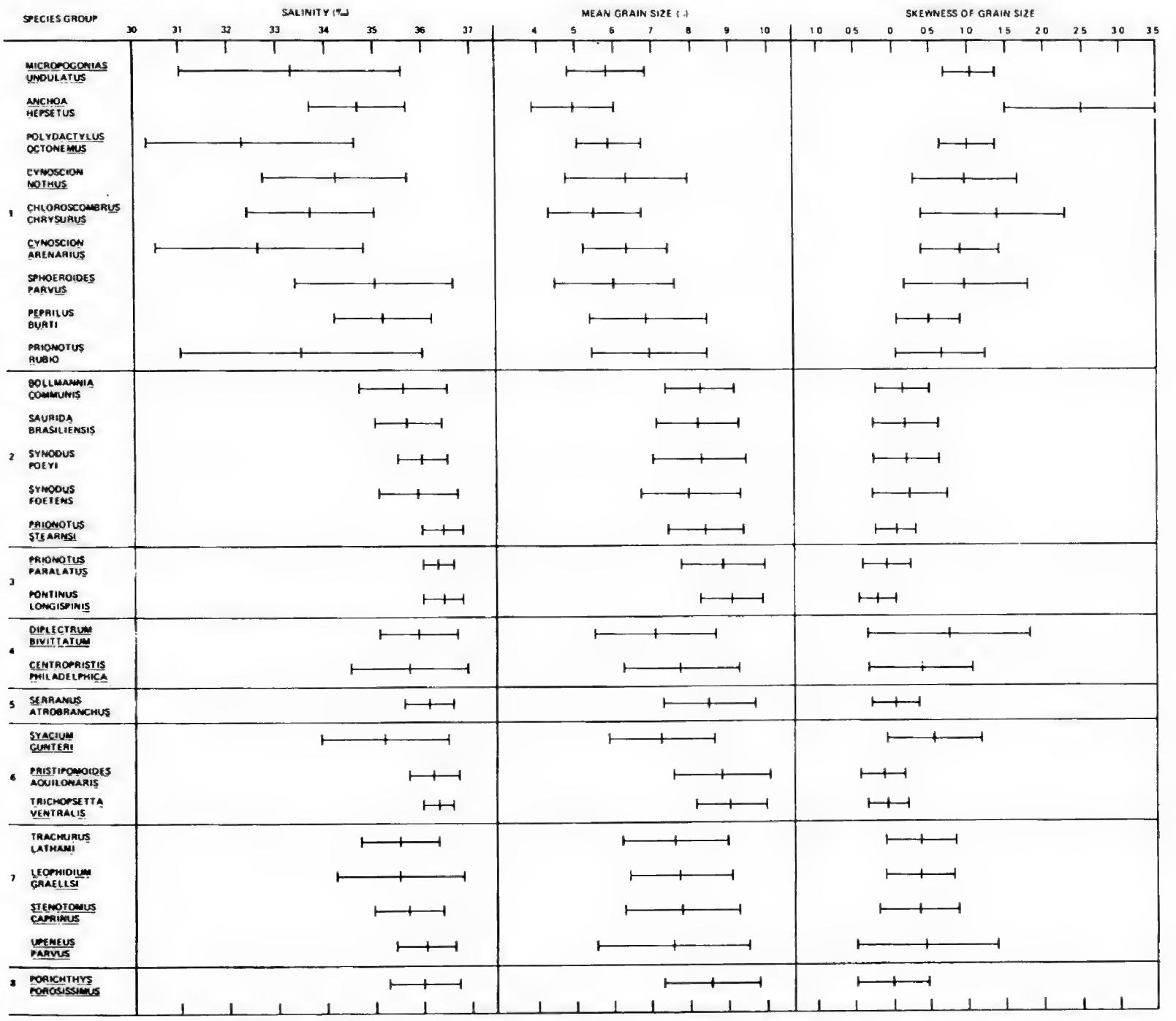


FIG. 6. Means ± 1 standard error for three physicochemical variables at which common fishes occurred. Species-groups were based on depth-distributions (Fig. 5).

Since several physicochemical variables change with depth, species that show differences in depth-distribution also will differ in their relationship to these variables. We compared the 27 most common fishes with respect to mean values and standard errors of three important physicochemical variables (identified from discriminant analysis) with which the fishes were associated (Fig. 6). Species occurring primarily on the inner shelf (species-group 1) tended to be associated with lower mean salinity values, but with greater variation in salinity than were mid-shelf or outer-shelf species. Within the inner-shelf species-group, there were notable differences in mean salinities at which the species occurred. The inner-shelf fishes also tended to occur over sediments with larger mean grain size (smaller $\phi$) and greater positive skewness of grain size, relative to other species-groups.

### Multiple Regression

Multiple regression of fish abundances on selected predictor variables explained for all species a statistically significant amount of variation in abundance ($p \leq 0.02$; ANOVA). The percentage of variation explained by regression (indicated by squared multiple-$R$) ranged from 8% to 57% (Table 6 for best regressions). The regression model was relatively ineffective in explaining variation in abundance of *Prionotus stearnsi* (8% explained variation), and somewhat more satisfactory for most other species (11–29%). The regression could be considered effective only for 9 of the 27 species examined (30–57% explained variation). The best regressions are those for *Bollmania communis* (57%), *Syacium gunteri* (48%) and *Anchoa hepsetus* (47%). Standard errors of residuals about the regression (S. E. in Table 6) varied widely, which attested to the differences among species in the effectiveness of the regressions.

In spite of the limited success shown by most of the regressions in accounting for variation in fish abundances, an idea of the relative importance of predictor variables can be gained. Of those predictor variables which explained (together with their powers) at least two percent of the variation in fish abundances, time of day did so for 14 species, depth for 11 species, and temperature for 10 species. Julian day, percent silt in the sediment, and abundance of epifaunal invertebrates each explained $\geq 2\%$ of the numerical variation in 9 different species. Mean sediment grain size, percent clay in the sediment, and diversity of infauna were each important for only one species.

## DISCUSSION

Earlier studies of the continental shelf ichthyofauna off Texas have generally treated relationships of fishes to environmental variables only in broad terms. Depth and temperature appear to have been the primary environmental correlates considered (*e.g.*, Miller 1965; Moore, Brusher, and Trent 1970; Chittenden and Moore 1977). A few studies have also mentioned sediment characteristics and day-night variability in captures (Caldwell

TABLE 6

**Summary of multiple regressions of fish abundances on selected biotic and abiotic predictor variables.[1] Only regressions explaining ≥ 25% of the variation in fish abundance are included. A multiple polynomial regression model was used with stepwise inclusion of variables (based on 298 data cases per species). The stepwise process entered all abiotic variables into the regression prior to inclusion of any biotic variables. All regressions were statistically significant (ANOVA; $P \leq 0.02$).**

| Species<br>Multiple-$R$ square[2] | S.E.[3] | Major predictor variables[4]<br>(% variation explained) | | | | | |
|---|---|---|---|---|---|---|---|
| *Anchoa hepsetus* | | % Sand | Mean grain size | | Skewness | | Abun. infa. |
| 0.47 | 38.85 | (14%) | (2%) | | (17%) | | (7%) |
| *Bollmania communis* | | Time | % Silt | Abun. epi. | | | |
| 0.57 | 1.87 | (4%) | (6%) | (38%) | | | |
| *Centropristis philadelphica* | | Time | Temperature | | % Silt | | Abun. epi. |
| 0.28 | 5.48 | (5%) | (4%) | | (7%) | | (8%) |
| *Chloroscombrus chrysurus* | | Temperature | | Salinity | Skewness | | Abun. infa. |
| 0.25 | 34.78 | (4%) | | (6%) | (3%) | | (3%) |
| *Cynoscion nothus* | | Transect | Depth | Temperature | Salinity | % Silt | Abun. epi. |
| 0.30 | 36.70 | (2%) | (4%) | (2%) | (10%) | (2%) | (3%) |
| *Lepophidium graellsi* | | Time | % Silt | Abun. epi. | | | |
| 0.34 | 1.13 | (9%) | (3%) | (14%) | | | |
| *Micropogon undulatus* | | Transect | Temperature | | Salinity | % Silt | |
| 0.26 | 81.93 | (3%) | (2%) | | (12%) | (2%) | |
| *Polydactylus octonemus* | | Temperature | | Salinity | % Silt | | |
| 0.29 | 39.49 | (3%) | | (16%) | (2%) | | |
| *Pontinus longispinis* | | Depth | % Sand | | | | |
| 0.35 | 2.11 | (26%) | (2%) | | | | |
| *Prionotus paralatus* | | Depth | Temperature | | Time | Julian day | |
| 0.25 | 11.02 | (9%) | (2%) | | (4%) | (5%) | |

**Table 6 (Continued)**

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Prionotus rubio* | | Time | Salinity | Abun. epi. | | | |
| 0.25 | 17.24 | (3%) | (10%) | (6%) | | | |
| *Pristipomoides aquilonaris* | | Depth | | | | | |
| 0.32 | 7.53 | (30%) | | | | | |
| *Serranus atrobranchus* | | Depth | Time | % Sand | No. epi. spp. | Abun. epi. | Div. infa. |
| 0.31 | 21.65 | (3%) | (5%) | (6%) | (3%) | (5%) | (2%) |
| *Syacium gunteri* | | Depth | Year | Time | No. epi. spp. | Abun. epi. | |
| 0.48 | 10.30 | (10%) | (4%) | (9%) | (2%) | (14%) | |
| *Trachurus lathami* | | Depth | Time | Julian day | Abun. epi. | | |
| 0.26 | 65.09 | (2%) | (4%) | (10%) | (3%) | | |
| *Trichopsetta ventralis* | | Depth | Year | Time | Julian day | No. epi. spp. | |
| 0.34 | 3.91 | (16%) | (3%) | (3%) | (3%) | (3%) | |

[1] Abiotic variables were transect, depth, Julian day, time of day, year, bottom-water temperature and salinity, mean grain size of sediment, standard deviation and skewness of sediment grain size, and percentages silt and sand in the sediment. Biotic variables were number of invertebrate epifauna species (No. epi. spp.), invertebrate epifauna abundance (Abun. epi.), invertebrate infauna diversity (Div. infa.), invertebrate infauna abundance (Abun. infa.), and organic carbon in the sediment.

[2] Multiple correlation coefficient squared, which represents the proportion of variation in each species' abundance explained by the multiple regression. Multiple-$R$ squared includes the contributions to the explained variance by the major predictor variables listed plus minor contributions by other variables.

[3] Standard error of residuals about the regression.

[4] Major predictor variables were those which together with their powers explained $\geq$ 2% of the total variation in species abundance (percentages given are variation explained by variables and their powers combined).

1955, Moore *et al.* 1970, Chittenden and McEachran 1976). Nonetheless, quantitative aspects of fish-environment relationships for this region are poorly known.

Our results from cluster and discriminant analyses indicated that there is a pronounced change with depth in ichthyofaunal composition on the continental shelf in the northwestern Gulf of Mexico. The results reinforce in a quantitative fashion similar statements made by other workers (Chittenden and McEachran 1976, Chittenden and Moore 1977). That abundances of some fishes (in trawls) change with depth was shown also by multiple regressions (Table 6).

The significance of cluster analysis lies not so much in corroborating earlier descriptions of this general depth change but in showing that this change, when examined in greater detail, is not a temporally stable pattern. There was noticeable variation between seasons and between years in the spatial distribution and abundances of species, which was reflected by the variation in ichthyofaunal composition at a given sampling locality. The variation indicated that the fish component of this ecosystem is relatively resilient in structure.

Discriminant analysis identified major abiotic variables and species (fishes and macroinvertebrates) that characterize the broadly defined depth-zones of the study area. For example, the most important abiotic factors discriminating between depth-zones were mean grain size and salinity. The inner-shelf zone was the easiest to identify abiotically because mean grain size was much coarser (mean $\phi$ = 5.90) there than in the mid- or outer-shelf zones (mean $\phi$ = 7.86 and 8.95) and salinity was lower and more variable. The identification of key parameters and components in the present analysis should serve to achieve greater efficiency of sampling design by focusing on these key features in future studies on this system. Discriminant analysis further served to identify major factors that were related (statistically) to changes in the ichthyofauna and to suggestions of possible functional relationships. However, a still wider array of variables was shown by multiple regressions to be important.

Finally, discriminant analysis provided a quantitative basis for the division of the Gulf shallow-water ichthyofauna into two components by depth, which are historically referred to as the "white shrimp ground" and "brown shrimp ground" faunas (Hildebrand 1954, Chittenden and McEachran 1976). Division of the faunas at 25–30 meters follows that of other workers, although the results from cluster analysis indicated that this boundary cannot be regarded as fixed over time. Biotically, the shallow, inner-shelf region was characterized by the dominance of *Micropogonias undulatus, Peprilus burti* and *Cynoscion nothus,* and by the virtual absence of *Serranus atrobranchus,* the second most abundant fish taken in the study. Our analysis also indicated a strong faunal division at about 90 meters based on a group of deep-water species not regularly encountered on the brown shrimp grounds (mid-shelf). These species included *Pontinus longispinis, Decodon puellaris, Ancylopsetta dilecta, Priancanthus arenatus, Equestus acuminatus, Heman-*

*thias vivanus,* and *Urophycis cirratus.* This outer boundary apparently corresponds to the transitional area between the mid-shelf (30–90 m) and continental slope faunas suggested by Chittenden and McEachran (1976).

The influence of sediment characteristics on Gulf fish distributions has been recognized in earlier studies (Springer and Bullis 1954, Miller 1959, Dawson 1964) that describe distinct fish assemblages for different bottom types—calcareous (pink shrimp grounds) and terrigenous mud (brown shrimp grounds). Variation between seasons in ichthyofaunal composition indicated by cluster analysis agrees with the fact that some species (*e.g., Micropogonias undulatus, Peprilus burti*) undergo regular migrations into bays or shallow water (Gunter 1945). Also, day-night differences in ichthyofaunal composition shown by cluster analysis are consistent with the results of Vetter (1978; using the same data we used) and of workers in other areas (Konstantinov 1964; Parrish, Blaxter, and Hall 1964; Woodhead 1964) who showed substantial diel differences in trawled abundances for a wide variety of fishes.

We stress that the relationships which have emerged from this analysis are purely statistical in nature, and not all of them may have actual biological meaning. The lack of detailed biological information on most of the species makes the assessment of the functional significance of some environmental variables to fishes difficult. For example, it is unclear why certain sediment characteristics are important in explaining variation in abundance of *Anchoa hepsetus* (Table 6). It may be that sediment is actually not directly important to *Anchoa hepsetus,* but is highly correlated with some other factors (possibly not measured) which affect fish abundance. On the other hand, some statistical associations indicated here may reflect relationships of biological significance which have not yet been recognized or appreciated, and they thus serve to point out areas which perhaps warrant closer study.

However, given that most of the observed statistical relationships have actual ecological relevance, the results of multiple regressions (Table 6) probably are the most useful in indicating possible causative relationships among environmental variables and fish abundances. Thus, Julian day may be important for *Prionotus paralatus* because of seasonal trends in abundance of this species (*e.g.*, seasonal movements or recruitment of young). Invertebrate epifaunal abundance may be important for *Bollmania communis* and *Syacium gunteri* because it possibly reflects the available food supply (both species feed on the bottom to some extent; Rogers 1977). The elucidation of such relationships lies beyond the aims of this study. Clearly, more direct ecological studies are needed.

As a cautionary note, we point out that the detailed results of the regression analyses are specific to the data set employed. Although the identification of (statistically) important predictor variables for this system can be accepted with a fair degree of confidence, the relative importance of the predictors as indicated by the regressions should be viewed as approximate. Also, the regressions provided reasonably accurate descriptions of fish abundances for only 9 out of 27 species examined, and for none of the

species did the amount of variation in abundance explained by regression exceed 57%. Perhaps the failure to obtain more accurate descriptions was inevitable, given the scope and design of the survey sampling program. An attempt to cover such a large area over a three-year period necessarily sacrificed the degree of resolution that is desirable for an accurate assessment of population-environment relationships. Obtaining more accurate results which are also amenable to direct biological interpretation will require more detailed and circumscribed studies. At present, we are limited to identifying broad statistical trends which perhaps later may be shown to represent functional relationships between fishes and their environment.

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## REFERENCES

AFIFI, A. A. and S. P. AZEN. 1972. Statistical analysis. *A Computer Oriented Approach.* Academic Press, NY.

ANDERBERG, M. R. 1972. *Cluster Analysis for Applications.* Wiley, NY.

CALDWELL, D. K. 1955. Distribution of the longspined porgy *Stenotomus caprinus. Bulletin of Marine Science Gulf and Caribbean.* 5:230–239.

CHITTENDEN, M. E., JR. and J. D. McEACHRAN. 1976. Composition, ecology and dynamics of demersal fish communities on the northwestern Gulf of Mexico continental shelf, with a similar synopsis for the entire Gulf. Sea Grant Publication. TAMU-SG-76-208.

_____ and D. MOORE. 1977. Composition of the ichthyofauna inhabiting the 110-meter bathymetric contour of the Gulf of Mexico, Mississippi River to the Rio Grande. *Northeast Gulf Science.* 1:106–114.

CLIFFORD, H. T. and W. STEPHENSON. 1975. *An Introduction to Numerical Classification.* Academic Press, NY.

DAWSON, C. E. 1964. A revision of the western Atlantic flatfish genus *Gymnachirus* (the naked soles). *Copeia.* 1964:646–665.

FLINT, R. W. and C. W. GRIFFIN, eds. 1979. Environmental studies, south Texas outer continental shelf, biology and chemistry. Contract AA550-CT7-11. *1977 Final Report to the Bureau of Land Management.* Washington, D.C.

_____ and N. N. RABALAIS, eds. 1980. Environmental studies, south Texas outer continental shelf, 1975-1977. Contract AA551-CT8-51. *Report to the Bureau of Land Management,* Washington, D.C.

GROOVER, E. D., ed. 1977. Environmental studies, south Texas outer continental shelf, biology and chemistry. Contract AA550-CT6-17. *1976 Final report to the Bureau of Land Management,* Washington, D.C.

GUNTER, G. 1945. Marine fishes of Texas. *Publications of the Institute of Marine Science, University of Texas.* 1:1–190.

HILDEBRAND, H. H. 1954. A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. *Publications of the Institute of Marine Science, University of Texas.* **3**:229–366.

HOLLAND, J. S., JR. 1977. Invertebrate epifauna and macrofauna. In R. D. Groover, editor. Environmental studies, south Texas outer continental shelf, biology and chemistry. Contract AA550-CT6-17. 1976 Final report to the Bureau of Land Management, Washington, D.C.

KLECKA, W. R. 1975. Discriminant analysis. In N. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Brent (eds.). *SPSS: Statistical Package for the Social Sciences.* McGraw-Hill, NY.

KONSTANTINOV, K. G. 1964. Diurnal vertical migrations of demersal fish and their possible influence on the estimation of fish stocks. *Rapports et Proces-Verbaux des Reunions, Conseil Permanent International pour l'Exploration de la Mer.* **155**:23–26.

LANCE, G. N. and W. T. WILLIAMS. 1967a. Mixed-data classificatory programs. I. Agglomerative systems. *Australian Computer Journal.* **1**:15–20.

LANCE, G. N. and W. T. WILLIAMS. 1967b. A general theory of classificatory sorting strategies. I. Hierarchical systems. *Computer Journal.* **9**:373–380.

LEWIS, T. C. and R. W. YERGER. 1976. Biology of five species of sea robins (*Pisces, Triglidae*) from the northeastern Gulf of Mexico. *Fishery Bulletin.* **74**:93–103.

MILLER, J. M. 1965. A trawl study of the shallow Gulf fishes near Port Aransas, Texas. *Publications of the Institute of Marine Science, University of Texas.* **10**:80–108.

MILLER, R. J. 1959. A review of the sea basses of the genus *Centropristes* (Serranidae). *Tulane Studies in Zoology and Botany.* **7**:35–68.

MOORE, D. H., A. BRUSHER and L. TRENT. 1970. Relative abundance, seasonal distribution and species composition of demersal fishes off Louisiana and Texas, 1962–1964. *Contributions in Marine Science.* **15**:45–70.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER and D. H. BRENT, eds. 1975. *SPSS: Statistical Package for the Social Sciences.* 2nd ed. McGraw-Hill, NY.

PARKER, P. L., ed. 1976. Environmental studies, south Texas outer continental shelf, biology and chemistry. Contract AA550-CT5-16. 1975 Final report to the Bureau of Land Management, Washington, D.C.

PARRISH, B. B., J. H. S. BLAXTER and W. B. HALL. 1964. Diurnal variations in size and composition of trawl catches. *Rapports et Proces-Verbaux des Reunions, Conseil Permanent International pour l'Exploration de la Mer.* **155**:27–34.

ROGERS, R. M., JR. 1977. Trophic interrelationships of selected fishes on the continental shelf of the northern Gulf of Mexico. Ph.D. Thesis, Texas A & M University, College Station.

SOKAL, R. R. and F. J. ROHLF. 1969. *Biometry; The Principles and Practice of Statistics in Biological Research.* Freeman, San Francisco, CA. 776 p.

SPRINGER, S. and H. BULLIS, JR. 1954. Exploratory shrimp fishing in the Gulf of Mexico, summary report for 1952–54. *Commercial Fisheries Review.* **16**:1–16.

TATSUOKA, M. M. 1971. *Multivariate Analysis: Techniques for Educational and Psychological Research.* Wiley, NY.

VETTER, E. F. 1978. Diel variations in trawl vulnerability of ichthyofaunal species from the south Texas outer continental shelf. M.S. Thesis, Univ. of Texas, Austin.

WOHLSCHLAG, D. E. 1976. Demersal fishes. In P. L. Parker, ed. Environmental Studies, South Texas Outer Continental Shelf, Biology and Chemistry. Contract AA550-CT5-16. 1975 Final report to the Bureau of Land Management, Washington, D.C.

———. 1977. Demersal fishes. In R. D. Groover, ed. Environmental Studies, South Texas Outer Continental Shelf, Biology and Chemistry. Contract AA550-CT6-17. 1976 Final report to the Bureau of Land Management, Washington, D.C.

———. 1979. Demersal fishes. In R. W. Flint and C. W. Griffin, eds. Environmental Studies, South Texas Outer Continental Shelf, Biology and Chemistry. Contract AA550-CT7-11. 1977 Final report to the Bureau of Land Management, Washington, D.C.

WOODHEAD, P. M. J. 1964. Diurnal changes in trawl catches in fishes. *Rapports et Proces-Verbaux des Reunions, Conseil Permanent International pour l'Exploration de la Mer.* **155**:35–44.

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# RED DRUM (*SCIAENOPS OCELLATUS*) MOVEMENT IN TEXAS BAYS

Hal R. Osburn, Gary C. Matlock, and Albert W. Green

*Texas Parks and Wildlife Department,*
*P. O. Box 1707, Rockport, Texas 78382*

## ABSTRACT

Red drum movement in Texas bays was studied by means of fish tagged with internal abdominal anchor tags and subsequently released. Intrabay movement was minimal with the majority (>71%) of returned tagged red drum moving ≤10 km. Few fish were returned from the Gulf or from outside the bay in which they were tagged. Movement patterns of red drum, however, differed significantly among some bay systems. There was no detectable relation between minimum distance moved by red drum and seasons or size of fish. The previously reported mass migration of red drum in winter was not detected in this study. Texas bay systems can be considered closed systems for fish ~305–625 mm TL when managing red drum stocks. Due to the restricted movement patterns, local populations of red drum could be vulnerable to intense fishing pressure.

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## INTRODUCTION

Red drum (*Sciaenops ocellatus*) is an important recreational and commercial resource on the Texas coast. During September 1974–August 1976, recreational fishermen landed 309,000 kg of red drum annually from Texas bays; the commercial harvest reached a record 953,000 kg in 1975 (Heffernan, Green, McEachron, Weixelman, Hammerschmidt and Harrington 1976; Breuer, Benefield, Weixelman, Martinez and Nava 1977).

Effective management of the red drum fishery requires an understanding of the species' growth, mortality and movement patterns. A coastwide finfish monitoring and tagging program was begun in November 1975 by the Texas Parks and Wildlife Department (TPWD). The purpose of this paper is to present red drum movement data from the first 3 years of this tagging project. Specifically addressed are the general pattern and extent of red drum movement, the differences in movement of fish in each bay system, the extent of intrabay, interbay and bay-Gulf movement and the effects of seasons and fish size on movement.

Tagging studies in Florida bays indicated that >85% of the recaptured red drum moved <10 km from the tagging site (Ingle, Hutton and Topp 1962; Beaumariage and Wittich 1966; Beaumariage 1969). Simmons and Breuer (1962) also reported little intrabay movement of red drum from Aransas Bay,

Texas southward. Based on red drum netted in the Corpus Christi and Aransas Bay systems, Pearson (1929) and Gunter (1945) described an exodus of red drum from the bays to the Gulf of Mexico in the fall and a return in the late winter or early spring. Simmons and Breuer (1962) concurred with this seasonal migration theory but noted that it was less pronounced and covered shorter periods of time than previously reported. Additional tagging studies have been conducted in Texas bays during the past 30 years, but comprehensive and comparable data for red drum in the various bay systems are lacking (Matlock and Weaver 1979).

## MATERIALS AND METHODS

Red drum for tagging were obtained during gill net and trammel net sampling in the Galveston, East Matagorda, Matagorda, San Antonio, Aransas, Corpus Christi, upper Laguna Madre and lower Laguna Madre Bay systems during November 1975–September 1978 (Fig. 1). Monofilament gill nets of 7.6-, 10.2-, 12.7- and 15.2-cm stretched mesh and multifilament trammel nets of 7.6-cm stretched mesh in the inner wall were set at randomly selected sites in each bay system.

Internal abdominal tags with an external streamer were inserted in apparently healthy fish using a technique described by Moffett (1961). Prior to release the total length (TL) of each fish was measured to the nearest mm. Tags were made of semi-hard glossy blue, red or green plastic (25.4 x 6.4 x 0.8 mm) with round corners. Each tag was uniquely numbered and bore the legend "TEXAS PWD, ROCKPORT" or "TEXAS PWD, SEABROOK". The external streamer consisted of a section of bright yellow flexible plastic hollow tubing (~50 mm long; O. D. = 2.1 mm; I. D. = 1.0 mm) which extended from a single hole in the center of each tag.

To improve return rates, the tagging program was publicized through the use of radio, television, newspapers and magazines as well as tagging posters distributed to places frequented by recreational and commercial fishermen. As an incentive for fishermen to return recovered tags a $1–$25 reward was paid by the National Marine Fisheries Service or the Gulf Coast Conservation Association regardless of the amount of information provided. Each individual returning a tag was requested to furnish the exact size (total length and/or weight) and the date and location of catch.

Minimum distances moved by red drum were obtained by plotting the tagging and recapture sites and measuring the shortest aquatic distance (to the nearest km) between the two sites. Time free (to the nearest day) was the time between tagging and recapture excluding the date tagged and including the date recaptured.

A single classification analysis of variance (Sokal and Rohlf 1969) was used to compare the mean lengths of tagged and untagged red drum captured in the routine netting samples in each bay system.

Differences in the pattern of bay-Gulf and interbay movement by fish in each bay system were determined using a test of independence (G-statistic) (Sokal and Rohlf 1969). Differences in the pattern of intrabay movement were determined by comparing the number of fish moving within each 5-km increment from the tagging site in each bay system using the G-statistic.

Relationships between distance moved *vs.* season and size at tagging were examined by plotting the combined data from the bay systems in which the pattern of intrabay movement was similar. Red drum recaptures originally released during the same month or season were plotted together against distance moved to detect a possible migration away from and return to a specific locale. Directional patterns were examined by plotting the angle and extent of net fish movement.

Assumptions for the movement data analyses include those reported by Osburn, Matlock and Hegen (1980). Briefly these were 1) that the return information from all fishermen was valid, 2) that there were no behavioral differences between tagged and untagged fish, and 3) that there was approximately equal fishing pressure and/or success in all areas where the fish may have moved.

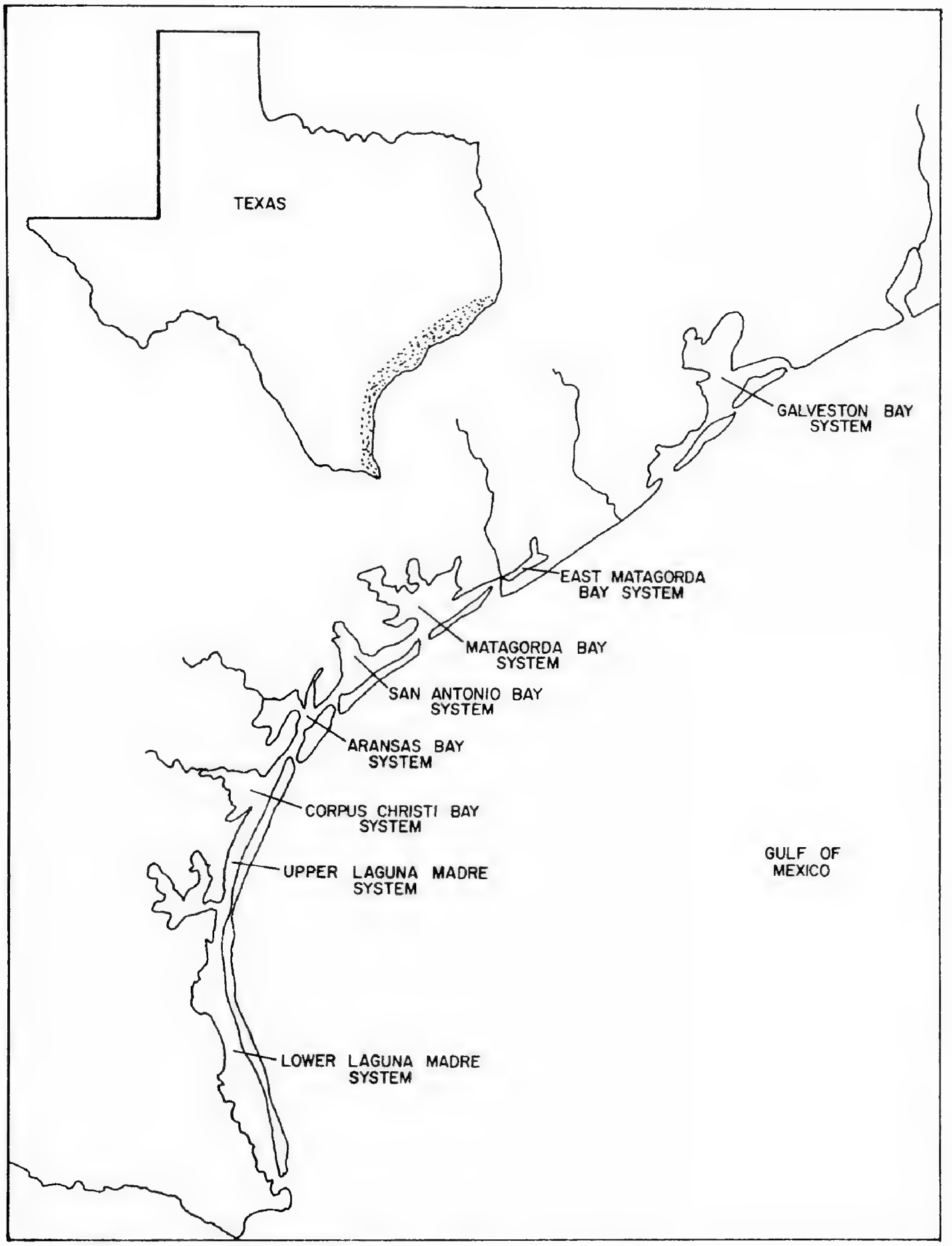


FIG. 1. Major bay systems on the Texas coast.

## RESULTS

From November 1975 through September 1978, 5519 red drum were tagged and released in Texas bays (Table 1). The mean size of red drum

TABLE 1

Number and size (total length in mm) of red drum captured in Texas bays during November 1975–September 1978.

| Bay system | Number | | Mean size ± 1 SD | | Size range | |
|---|---|---|---|---|---|---|
| | Untagged | Tagged | Untagged | Tagged | Untagged | Tagged |
| Galveston | 1262 | 659 | 459 ± 95 | 473 ± 96 | 250–780 | 205–836 |
| East Matagorda[1] | 128 | 182 | 439 ± 100 | 456 ± 100 | 291–840 | 183–708 |
| Matagorda | 1167 | 1338 | 444 ± 120 | 431 ± 154 | 196–763 | 240–924 |
| San Antonio | 858 | 961 | 375 ± 84 | 401 ± 83 | 218–760 | 209–735 |
| Aransas | 889 | 734 | 402 ± 94 | 412 ± 101 | 285–747 | 275–806 |
| Corpus Christi | 596 | 656 | 426 ± 91 | 410 ± 88 | 260–780 | 223–745 |
| Upper Laguna Madre | 350 | 276 | 429 ± 104 | 442 ± 107 | 268–784 | 200–805 |
| Lower Laguna Madre | 1299 | 713 | 459 ± 104 | 487 ± 101 | 255–750 | 255–732 |
| Coastwise | 6549 | 5519 | 433 ± 105 | 434 ± 116 | 196–840 | 183–924 |

[1]Fish were tagged during October 1976–September 1978.

tagged ranged from 401 ± 83 mm in the San Antonio Bay system to 487 ± 101 mm in the lower Laguna Madre system. The mean total length of tagged red drum was not significantly different from that of untagged red drum ($p>0.05$).

In each of the eight bay systems, most (>77%) of the recaptured red drum were caught in the same bay system in which they were originally tagged (Table 2). However, the proportion of fish leaving each bay system varied significantly among bays. Fish tagged in the Corpus Christi Bay and the upper Laguna Madre systems left these systems to a greater extent than fish tagged in the other six systems ($p<0.005$). However, 8 of the 25 Corpus Christi Bay system returns from outside that system were caught within 10 km of their tagging sites. If these are considered to be returns from the bay system where tagged, then the Corpus Christi Bay system, like the other six, is statistically different from the upper Laguna Madre ($p<0.005$). Red drum left the Galveston Bay system to a lesser extent than they did in all other systems ($p<0.005$). The coastwide tag return rate for red drum was 17.4% with 91.9% of all returns coming from the bay system where tagged.

The majority of red drum (51.9–80.8%) moved ≤10 km between their release and recapture sites in all bay systems (Table 3). Movement patterns of red drum, however, differed significantly among some bay systems. Movement patterns of fish in the Galveston, East Matagorda, Matagorda, San Antonio, Aransas and Corpus Christi Bay systems (Galveston-Corpus Christi) were not different from each other ($p>0.05$), but the pattern for fish

TABLE 2

**Interbay and bay-Gulf movement of tagged red drum returned during November 1975–September 1978.**

| Bay system where tagged | % of returns coming from | | | | | | | | | No. returned w/ data available on site of recapture |
|---|---|---|---|---|---|---|---|---|---|---|
| | Gal. | E. Mat. | Mat. | San Ant. | Aran. | Cor. Chr. | ULM | LLM | Gulf | |
| Galveston | 94.3 | 0.0 | 1.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.8 | 53 |
| East Matagorda[1] | 0.0 | 90.2 | 4.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.9 | 41 |
| Matagorda | 0.0 | 1.3 | 94.1 | 4.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 237 |
| San Antonio | 0.0 | 0.0 | 3.3 | 94.0 | 0.0 | 0.6 | 0.0 | 0.0 | 2.0 | 151 |
| Aransas | 0.0 | 0.0 | 1.4 | 0.0 | 97.2 | 1.4 | 0.0 | 0.0 | 0.0 | 141 |
| Corpus Christi | 0.0 | 0.0 | 0.0 | 0.0 | 10.4 | 81.5 | 7.4 | 0.0 | 0.7 | 135 |
| Upper Laguna Madre | 0.0 | 0.0 | 1.6 | 0.0 | 0.0 | 11.1 | 77.8 | 7.9 | 1.6 | 63 |
| Lower Laguna Madre | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 97.1 | 2.9 | 136 |

[1]Fish were tagged during October 1976-September 1978.

TABLE 3

**Percent of returned tagged red drum in relation to distance traveled from site of tagging during November 1975–September 1978.**

| Bay system group | Number with movement data available | Minimum distance traveled (km) | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 0-5 | 6-10 | 11-15 | 16-20 | 21-25 | 26.30 | > 30 |
| Galveston-Corpus Christi | 741 | 63.3 | 12.4 | 7.7 | 5.3 | 3.0 | 2.3 | 6.1 |
| Galveston | 52 | 65.4 | 15.4 | 7.7 | 3.8 | 0.0 | 1.9 | 5.8 |
| East Matagorda[1] | 41 | 58.5 | 14.6 | 9.8 | 7.3 | 0.0 | 0.0 | 9.8 |
| Matagorda | 237 | 66.7 | 12.2 | 5.9 | 3.0 | 3.8 | 1.3 | 7.2 |
| San Antonio | 140 | 60.0 | 11.4 | 5.7 | 9.3 | 2.9 | 5.0 | 5.7 |
| Aransas | 139 | 62.6 | 10.1 | 10.8 | 2.2 | 5.0 | 3.6 | 5.8 |
| Corpus Christi | 132 | 62.1 | 14.4 | 9.1 | 8.3 | 1.5 | 0.8 | 3.8 |
| Upper Laguna Madre | 63 | 42.9 | 12.7 | 3.2 | 4.8 | 3.2 | 7.9 | 25.4 |
| Lower Laguna Madre | 110 | 36.4 | 15.5 | 13.6 | 11.8 | 6.4 | 8.2 | 8.2 |

[1]Fish were tagged during October 1976-September 1978

movement in the upper Laguna Madre ($p<0.005$) and the lower Laguna Madre ($p<0.005$) was different from that of fish in the more northern bays as well as different from each other ($p<0.010$). Red drum movement in the Galveston-Corpus Christi group was more restricted than in the Laguna Madre, with 75.7% of the Galveston-Corpus Christi returns moving ≤10 km and only 6.1% moving >30 km. The large fraction (25.4%) of fish moving

>30 km in the upper Laguna Madre distinguished the movement pattern of fish in this system from that of fish in the lower Laguna Madre.

Distance moved by red drum in all bay systems was apparently unrelated to season or size of fish (Figs. 2–6). No relationships between time free and

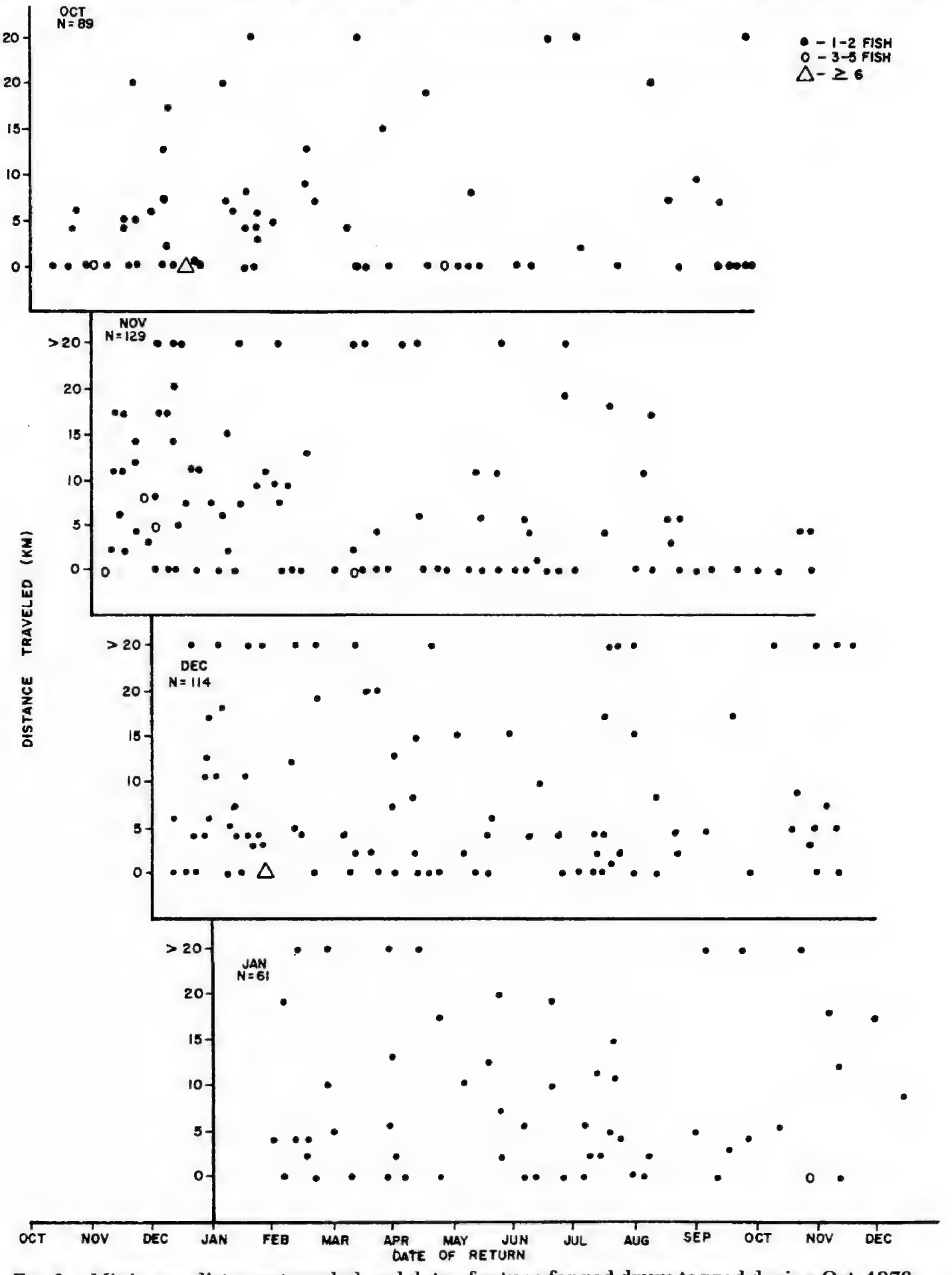


FIG. 2. Minimum distance traveled and date of return for red drum tagged during Oct. 1976–77, Nov. 1975–77, Dec. 1975–77 and Jan. 1976–78 in the Galveston-Corpus Christi Bay system group (first month in each graph indicates month of release).

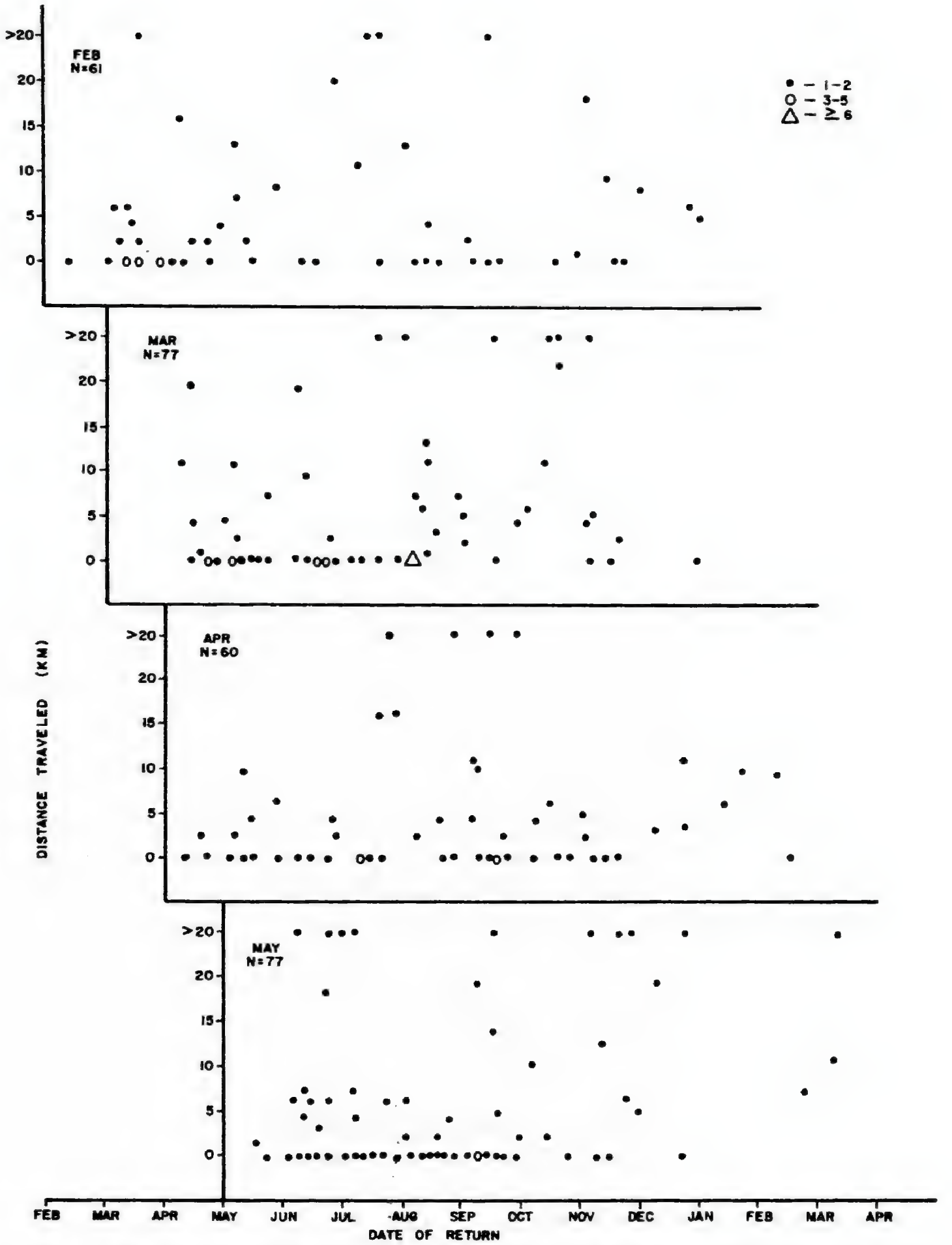


FIG. 3. Minimum distance traveled and date of return for red drum tagged during Feb.–May 1976–78 in the Galveston-Corpus Christi Bay system group (first month in each group indicates month of release).

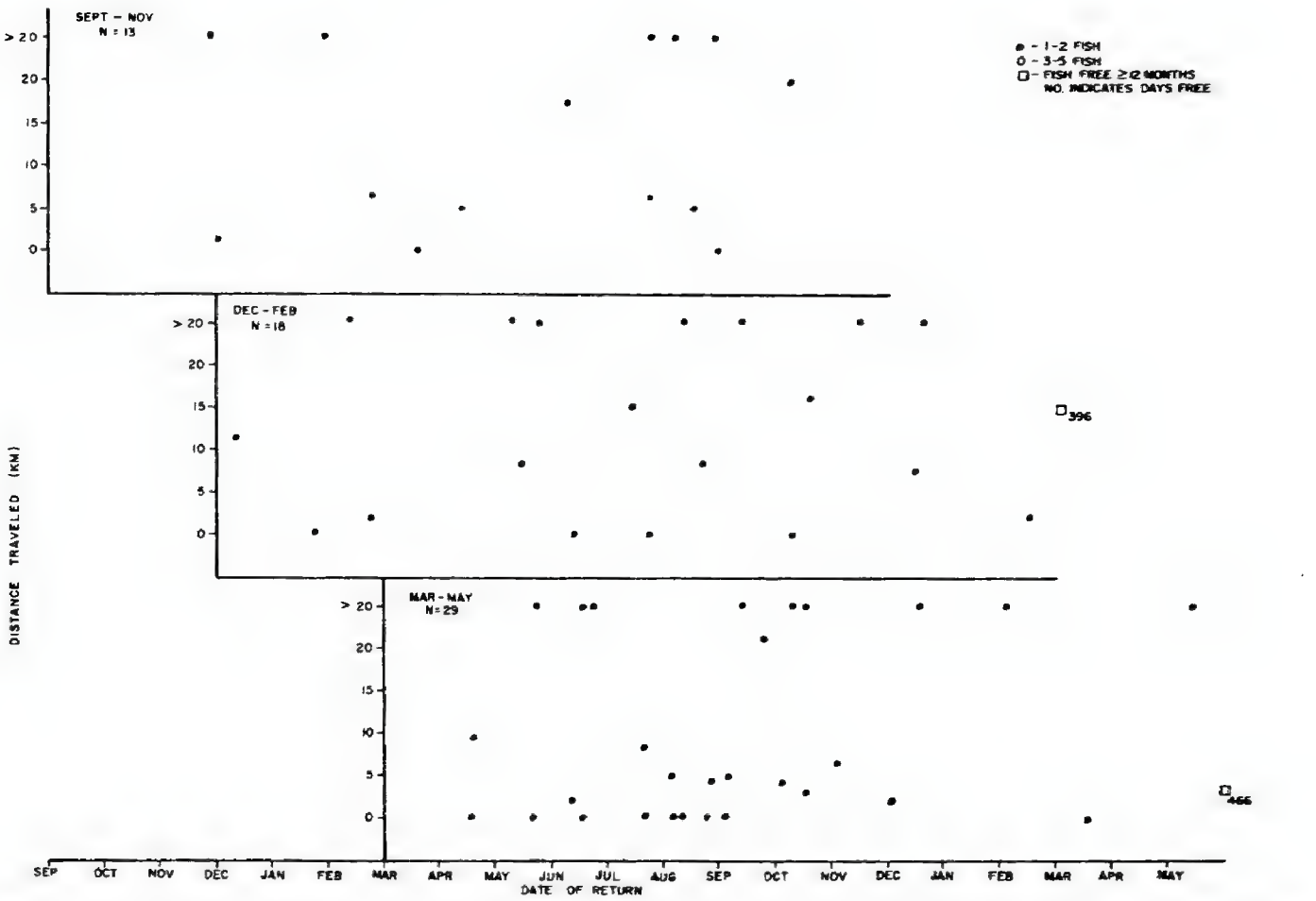


FIG. 4. Minimum distance traveled and date of return for red drum tagged during the fall 1975–78, winter 1975–77 and spring 1976–78 in the upper Laguna Madre (first three months in each graph indicates season of release).

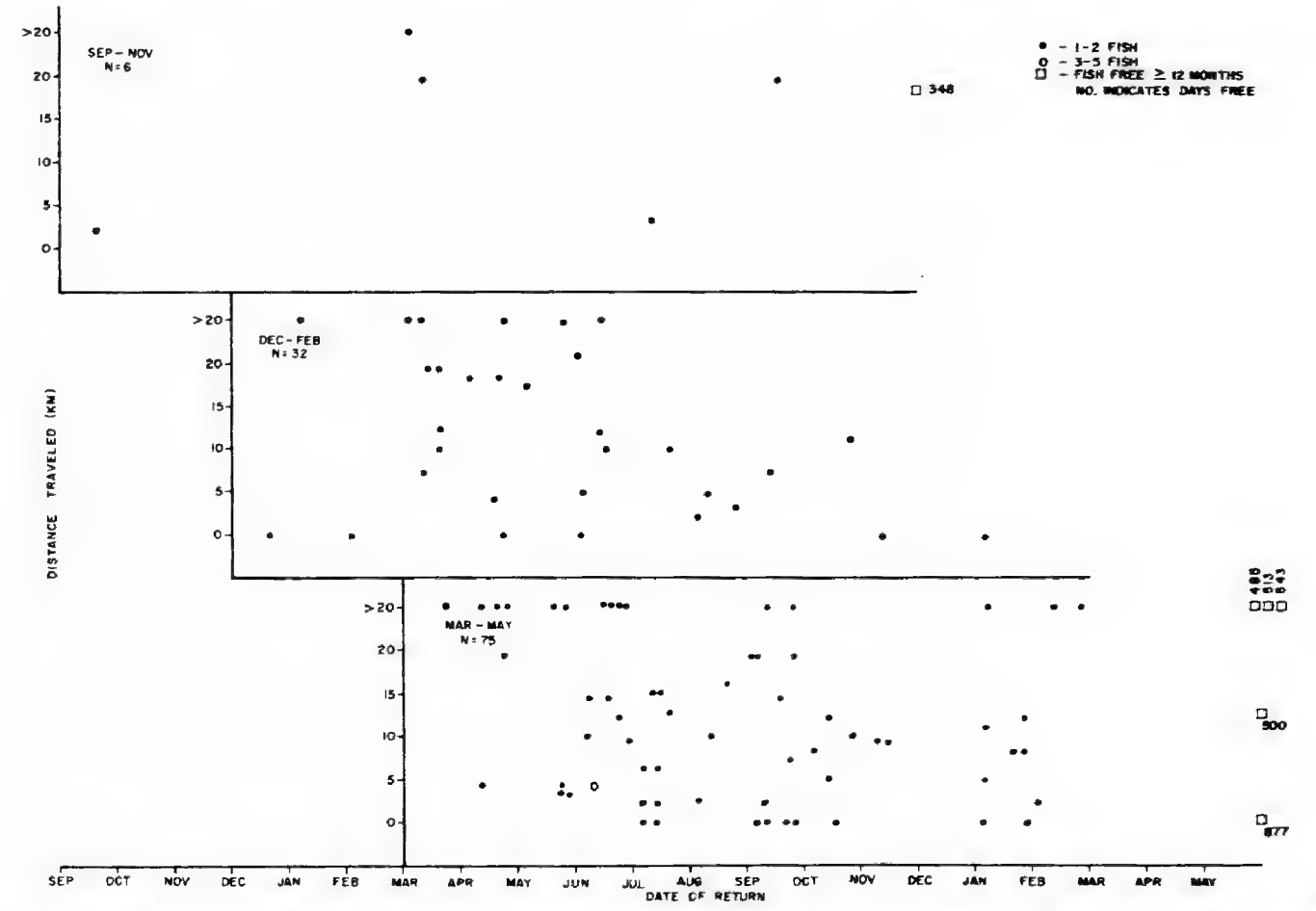


FIG. 5. Minimum distance traveled and date of return for red drum tagged during the fall 1975–78, winter 1975–77 and spring 1976–78 in the lower Laguna Madre (first three months in each graph indicates season of release).

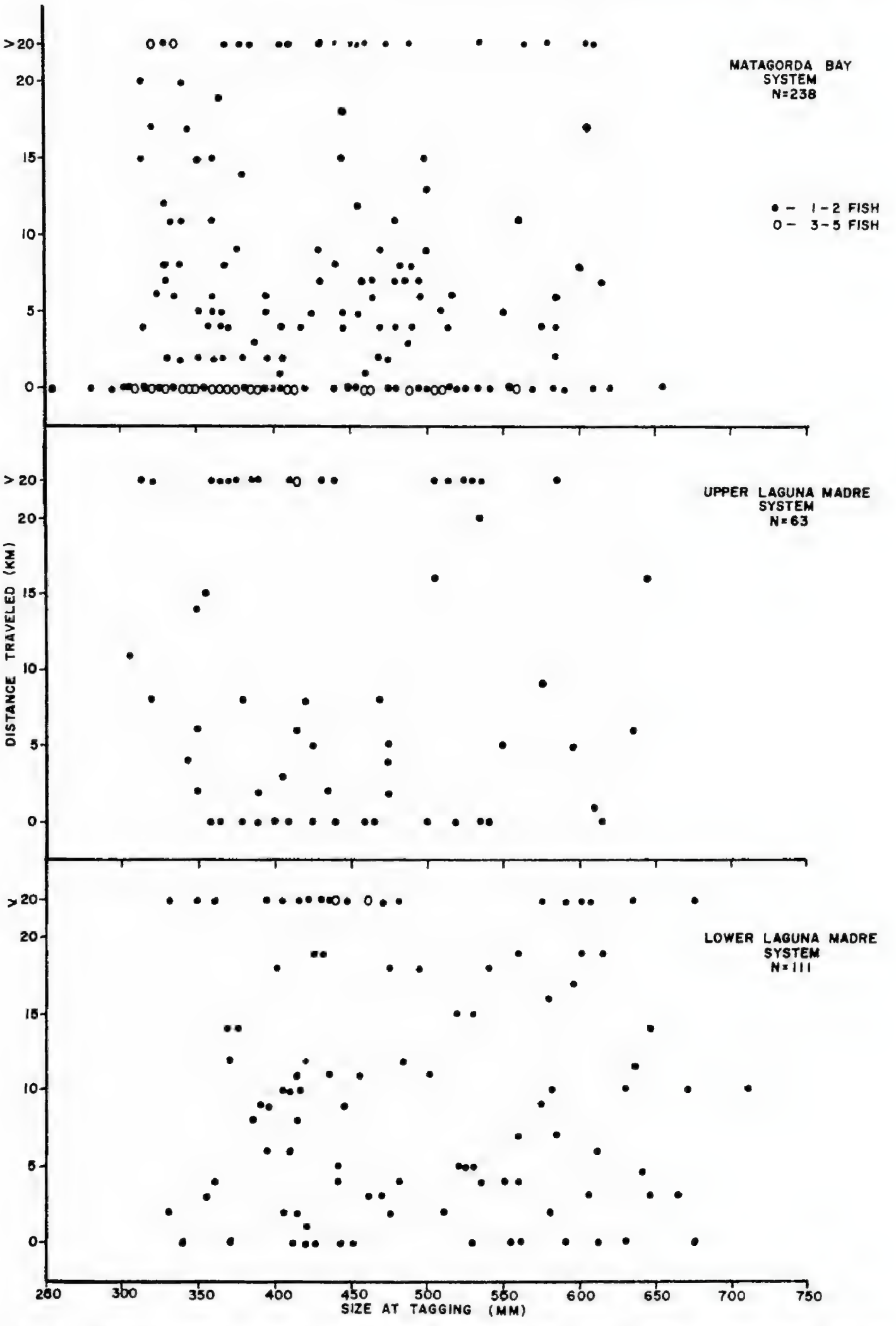


FIG. 6. Minimum distance traveled and size when released (total length in mm) for red drum tagged during Nov. 1975–Sept. 1978.

distance moved were evident. For those red drum that did move (>0 km), no definite directional patterns were discernible. Not plotted on Figs. 2 & 3 were 64 red drum returns that were free longer than 1 year; half of these were recaptured within 10 km of their tagging site.

Tag returns from the Gulf of Mexico constituted only 1.4% of the total coastwide returns (Table 4). Nearly all of the Gulf returns demonstrated

TABLE 4

Red drum tagged in Texas bays and returned from the Gulf of Mexico during November 1975–September 1978.

| Bay system where tagged | Date tagged | Date returned | Total length (mm) | | Direction of movement | Distance from tagging site to nearest Gulf pass (km) | Total distance moved (km) |
|---|---|---|---|---|---|---|---|
| | | | Release | Recapture | | | |
| Galveston | 5-28-76 | 9-15-76 | 590 | 635 | South | 10 | 35 |
| Galveston | 4-11-78 | 7-25-78 | 460 | - | East | 8 | 43 |
| East Matagorda | 10-19-76 | 12-01-77 | 532 | - | East | 4 | 104 |
| East Matagorda | 11-10-76 | 4-78 | 543 | - | West | 6 | 33 |
| San Antonio | 3-26-76 | 10-18-76 | 355 | 559 | South | 5 | 138 |
| San Antonio | 11-05-76 | 2-05-77 | 544 | 533 | North | 19 | 138 |
| San Antonio | 11-22-77 | 2-05-78 | 558 | 540 | North | 8 | 9 |
| Corpus Christi | 1-23-76 | 4-07-77 | 345 | - | North | 1 | 15 |
| Upper Laguna Madre | 2-27-76 | 5-07-76 | 415 | 445 | South | 11 | 50 |
| Lower Laguna Madre | 4-07-76 | 2-28-77 | 405 | - | East | 22 | 24 |
| Lower Laguna Madre | 12-10-76 | 3-09-77 | 670 | - | North | 4 | - |
| Lower Laguna Madre | 4-07-76 | 5-27-77 | 675 | - | South | 22 | 72 |
| Lower Laguna Madre | 12-10-76 | 10-30-77 | 500 | - | South | 4 | 11 |

considerably greater movement (69.2% moved >20 km) than their bay counterparts (14.5% moved >20 km). Of the 13 Gulf returns, 9 were tagged within 10 km of a Gulf pass.

## DISCUSSION

Red drum in Texas apparently spawn outside the estuaries in the Gulf of Mexico and/or the Gulf passes (Pearson 1929). The larvae are then carried by tidal currents through the passes into the estuaries (King 1971). Since few mature red drum have been noted in the bays (Pearson 1929, Gunter 1945, Simmons and Breuer 1962), a migration to the Gulf may occur as a fish reaches maturity, normally by the end of the fourth or fifth year (Pearson 1929). Movement of immature red drum in the bays, however, appears to be limited. In fact, for management purposes, each Texas bay system can be considered a closed system on an annual basis, after recruitment, for fish ~305–625 mm TL, i.e., Year Classes I–III (Pearson 1929). Simmons and

Breuer (1962) drew a similar conclusion (based on a limited number of tag returns) for the bays from Aransas Bay southward.

Many individuals in a school of immature red drum will apparently remain together at, or return frequently to, a single locale for at least several months. For example, of 86 red drum tagged and released on 26 October 1976 at one site in San Antonio Bay, 11 were recaptured by TPWD at the same site on 14 December 1976 and 4 were recaptured there on 25 April 1977 (TPWD unpublished data).

Due to such restricted movement patterns, local populations of red drum could be vulnerable to intense fishing pressure from rods and reels and particularly from more efficient gear such as gill nets and trammel nets. Based on limited data, Matlock, Weaver and Green (1977) concluded that lower red drum catch rates occurred in Texas bay areas open to commercial netting vs. areas closed to netting. Ingle *et al.* (1962) reported that with heavy sport fishing pressure, over 55% of the tagged red drum released in Florida bays were returned within 6 months. Heavy fishing mortality on Year Classes I–III from sport and commercial fishing interests may dictate that relatively few fish will survive to maturity in the bays. Of crucial importance, therefore, is the extent to which the bay populations of red drum provide recruitment to the spawning stock.

Despite limited knowledge of stock size and fishing characteristics in the Gulf of Mexico, the present study indicates no prominent seasonal migration to the Gulf for any of the size classes of red drum tagged in any of the bay systems sampled. Simmons and Breuer (1962), using a two-way fish trap, also found no pronounced migration of red drum during fall through a Texas Gulf pass (Cedar Bayou), although the authors suggested that deeper passes may be utilized. Breuer (1962) reported that red drum in Year Classes I–III "were abundant throughout the year on the flats" in the lower Laguna Madre system. Coffen (1975) stated that immature red drum were caught in deeper portions of the bays and coastal rivers in the winter. Matlock, Weaver, McEachron, Dailey, Hammerschmidt, Hegen, Harrington and Stokes (1978) found that red drum catches in gill nets declined in Texas bays during cold months and suggested that this decline could be due to movement of the fish to the Gulf, to deeper (>1.8 m) portions of the bays and/or to a reduction in fish activity. Year-round gill net sampling in Texas bays showed a decline in red drum catches during both winter and summer (Matlock and Weaver 1979). Movement of red drum to the unsampled deep water and moderate temperatures of the bays, and possibly rivers, in the winter when water temperatures decline (and in the summer when water temperatures rise) could account for the perhaps erroneous conclusions drawn by previous investigators concerning mass migrations of immature red drum out of the bays to the Gulf.

Simmons and Hoese (1959) reported tagging 134 red drum (mostly 400–460 mm TL) in April at the mouth of Cedar Bayou and receiving 30 returns—all from the Gulf. Heffernan (1973) sampled the Gulf surf zone with rod and reel, trotlines, and nets and caught mostly Year Class II red drum. Gunter (1958) caught red drum <100 mm in the Gulf surf between April and August,

which perhaps indicated that not all juveniles go to, or remain in, the bay nursery grounds. McFarland (1963) also seined red drum from the beach surf zone in the summer and reported that red drum were commonly caught in the surf by anglers. Simmons (1951) noted Gulf-to-bay movement of 203–254 mm TL red drum through the Cedar Bayou fish trap during summer. Restricted bay-Gulf movements of immature fish residing near passes may account for the presence of these fish in the Gulf. However, additional research is required to understand fully the relationships between immature fish in the Gulf and bays. Further study of red drum movement could make use of ultrasonic transmitters (Carr and Chaney 1977) to determine how routine such movements might be.

Despite their normally limited home range red drum can move great distances in a short time. Several tag returns indicated movement of 4–6 km per day over a 3–5 day period. The greatest distance moved by any returned red drum was 150 km in 417 days from the Aransas to the Matagorda Bay system. At least one fish in each bay system moved >50 km.

The greater movement of red drum in the Laguna Madre may be a reflection of the more extreme physio-chemical conditions of that area. The upper Laguna Madre system has been characterized as a hypersaline environment with relatively low nutrient concentrations due to limited freshwater inflow and inadequate water circulation because it contains no constant openings to the Gulf of Mexico (Simmons 1957). The lower Laguna Madre system has two passes to the Gulf and thus somewhat better water circulation so that hypersalinity is not so common (TPWD staff 1975, Breuer 1962). The peculiar environmental conditions of the Laguna Madre may thus result in a higher avoidance reaction by red drum and/or a greater dispersion of their food supply than in other Texas bay systems. Hawley's (1962) contention, however, that there is a southward migration of fishes from the upper Laguna Madre is not strictly supported by the present study because only 35% of all red drum returns tagged in the upper Laguna Madre moved south.

## ACKNOWLEDGMENTS

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## LITERATURE CITED

BEAUMARIAGE, D. S. 1969. Returns from the 1965 Schlitz tagging program including a cumulative analysis of previous results. *Florida State Board of Conservation, Technical Series.* No. 59. 38 p.

_____ and A. C. WITTICH. 1966. Returns from the 1964 Schlitz tagging program. *Florida State Board of Conservation, Technical Series.* No. 47. 50 p.

BREUER, J. P. 1962. An ecological survey of the lower Laguna Madre of Texas, 1953–1959. *Publications of the Institute of Marine Science, University of Texas.* 8:153–183.

———, R. L. BENEFIELD, M. G. WEIXELMAN, A. R. MARTINEZ and I. NAVA. 1977. Survey of finfish harvest in selected Texas bays. Segment II. Coast. Fish. Branch, Tex. Parks Wildl. Dept., Fed. Aid Completion Rept. Proj. 2-231-R-2. 115 p.

CARR, W. E. S. and T. B. CHANEY. 1977. Harness for attachment of an ultrasonic transmitter to the red drum, *Sciaenops ocellata*. *Fishery Bulletin.* 74(4):998–1000.

COFFEN, C. 1975. *Specks and redfish and how to catch'em.* Double C. Productions, Inc., Houston, Tex. 169 p.

GUNTER, G. 1945. Studies on marine fishes of Texas. *Publications of the Institute of Marine Science, University of Texas.* 1(1):1–190.

———. 1958. Population studies of the shallow water fishes of an outer beach in south Texas. *Publications of the Institute of Marine Science, University of Texas.* 5:186–193.

HAWLEY, W. 1962. Population studies of the sports and commercial finfish and forage species of the upper Laguna Madre. *Texas Game and Fish Commission, Coastal Fisheries Project Reports.* 1961–62. (mimeo).

HEFFERNAN, T. L. 1973. Survey of adult red drum. *Texas Parks and Wildlife Department, Coastal Fisheries Project Reports.* 1973. p.37–66.

———, A. W. GREEN, L. W. McEACHRON, M. G. WEIXELMAN, P. C. HAMMERSCHMIDT and R. A. HARRINGTON. 1976. Survey of finfish in selected Texas bays. Coast. Fish. Branch, Tex. Parks Wildl. Dept., Fed. Aid Completion Rept. Proj. 2-231-R-1. 116 p.

INGLE, R. M., R. F. HUTTON and R. W. TOPP. 1962. Results of the tagging of salt water fishes in Florida. *Florida State Board of Conservation, Technical Series. No.* 38. 57 p.

KING, B. D. III 1971. Study of migratory patterns of fish and shellfish through a natural pass. *Coastal Fisheries Branch, Texas Parks and Wildlife Department, Technical Series.* No. 9. 54 p.

MATLOCK, G. C. and J. E. WEAVER. 1979. Fish tagging in Texas bays during Nov. 1975–Sept. 1976. *Coastal Fisheries Branch, Texas Parks and Wildlife Department, Management Data Series. No.* 1. 135 p.

———, ——— and A. W. GREEN. 1977. Trends in spotted seatrout and red drum abundance in Texas coastal waters influenced by commercial netting activities. *Proceedings. Annual Conference Southeastern Association Game and Fish Commission.* 31:477–483.

———, ———, L. W. McEACHRON, J. A. DAILEY, P. C. HAMMERSCHMIDT, H. E. HEGEN, R. A. HARRINGTON and G. M. STOKES. 1978. Trends in finfish abundance in Texas estuaries as indicated by gill nets. Coast. Fish. Branch, Tex. Parks Wildl. Dept. 271 p. (unpubl. report)

McFARLAND, W. N. 1963. Seasonal change in the number and the biomass of fishes from the surf at Mustang Island, Texas. *Publications of the Institute of Marine Science, University of Texas.* 9:91–105.

MOFFETT, A. W. 1961. Movements and growth of spotted seatrout, *Cynoscion nebulosus* (Cuvier), in west Florida. *Florida State Board of Conservation, Technical Series.* No. 36. 35 p.

OSBURN, H. R., G. C. MATLOCK and H. E. HEGEN. 1980. Description of a multiple census tagging program for marine fisheries management. Ann. Proc. of the Tex. Chap. Amer. Fish. Soc. Vol. 2. pp. 9–25.

PEARSON, J. S. 1929. Natural history and conservation of redfish and other commercial sciaenids of the Texas coast. *Bulletin of the Bureau of Fisheries.* 44:129–214.

SIMMONS, E. G. 1951. The Cedar Bayou fish trap. *Texas Game and Fish Commission, Coastal Fisheries Project Reports.* 1950–1951:1–26 (mimeo).

———. 1957. An ecological survey of the upper Laguna Madre of Texas. *Publications of the Institute of Marine Science, University of Texas.* 4(2):156–203.

——— and J. P. BREUER. 1962. A study of redfish, *Sciaenops ocellata* and black drum, *Pogonias cromis. Publications of the Institute of Marine Science, University of Texas.* 8:184–211.

——— and H. D. HOESE. 1959. Studies on the hydrography and fish migration of Cedar Bayou, a natural tidal inlet on the central Texas coast. *Publications of the Institute of Marine Science, University of Texas.* 6:56–80.

SOKAL, R. R. and F. J. ROHLF. 1969. *Biometry.* W. H. Freeman and Co. 776 p.

TPWD STAFF. 1975. Fishery resources of the lower Laguna Madre and factors relating to their viability. Preliminary Draft. Coastal Fisheries Branch. (unpubl. report)

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# BEHAVIORAL ECOLOGY OF NORTHERN ADRIATIC REEF FISHES IN RELATION TO SEASONAL TEMPERATURE REGIMES

Kurt Kotrschal[1] and William W. Reynolds[2]

## ABSTRACT

Observations by scuba diving of shallow sublittoral reef fishes in the northern Adriatic during the winter indicate that these fishes remain in their reef habitats throughout the winter. Many of them, particularly those of tropical affinities, become inactive and remain under cover at low (7–10°C) winter temperatures. Littoral tidepools are abandoned at the lowest (near-freezing) temperatures, but there is no migration of reef fishes to deeper and slightly warmer (12.5°C) sublittoral waters, where reef habitats are unavailable in the northern Adriatic.

Cold-tolerant predators such as *Scorpaena ustulata* feed opportunistically on cold-numbed prey species. Different thermal tolerances and optima, reflected by spawning and other activity maxima at different times of the year, suggest that seasonal shifts in interspecific interactions among the reef fish species are influenced largely by temperature.

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## INTRODUCTION

The northern Adriatic portion of the Mediterranean Sea is an environment of extensive seasonal temperature changes in the littoral and shallow sublittoral zones (Zore-Armanda 1968, Fig. 1). Monthly mean sea surface temperatures range from a low of 9°C in February to 26°C in August; extreme values range from 7° to 28°C. In this paper, we examine some aspects of the behavior of Adriatic shallow-water fishes in relation to this environmental thermal variation.

Fishes generally are ectotherms which, by definition, exert little or no physiological control over their internal body temperatures (Reynolds 1979); there are, however, some notable exceptions among the Scombridae and Lamnidae. Ectotherms thermoregulate primarily by behavioral means to select favorable environmental temperatures which are then closely approximated by their internal body temperatures (Reynolds and Casterlin 1979, 1980). When environmental conditions are unsuitable for behavioral thermoregulation, as when appropriate thermal heterogeneity is lacking or when other ecological factors are of overriding importance, ectotherms have available the alternative option of thermal acclimation or acclimatiza-

[1]*Zoologisches Institut der Universität Salzburg, A-5020 Salzburg, Austria*
[2]*BioThermal Research Institute, R.D. 3, Box 10, Wyoming, PA 18644, U.S.A.*

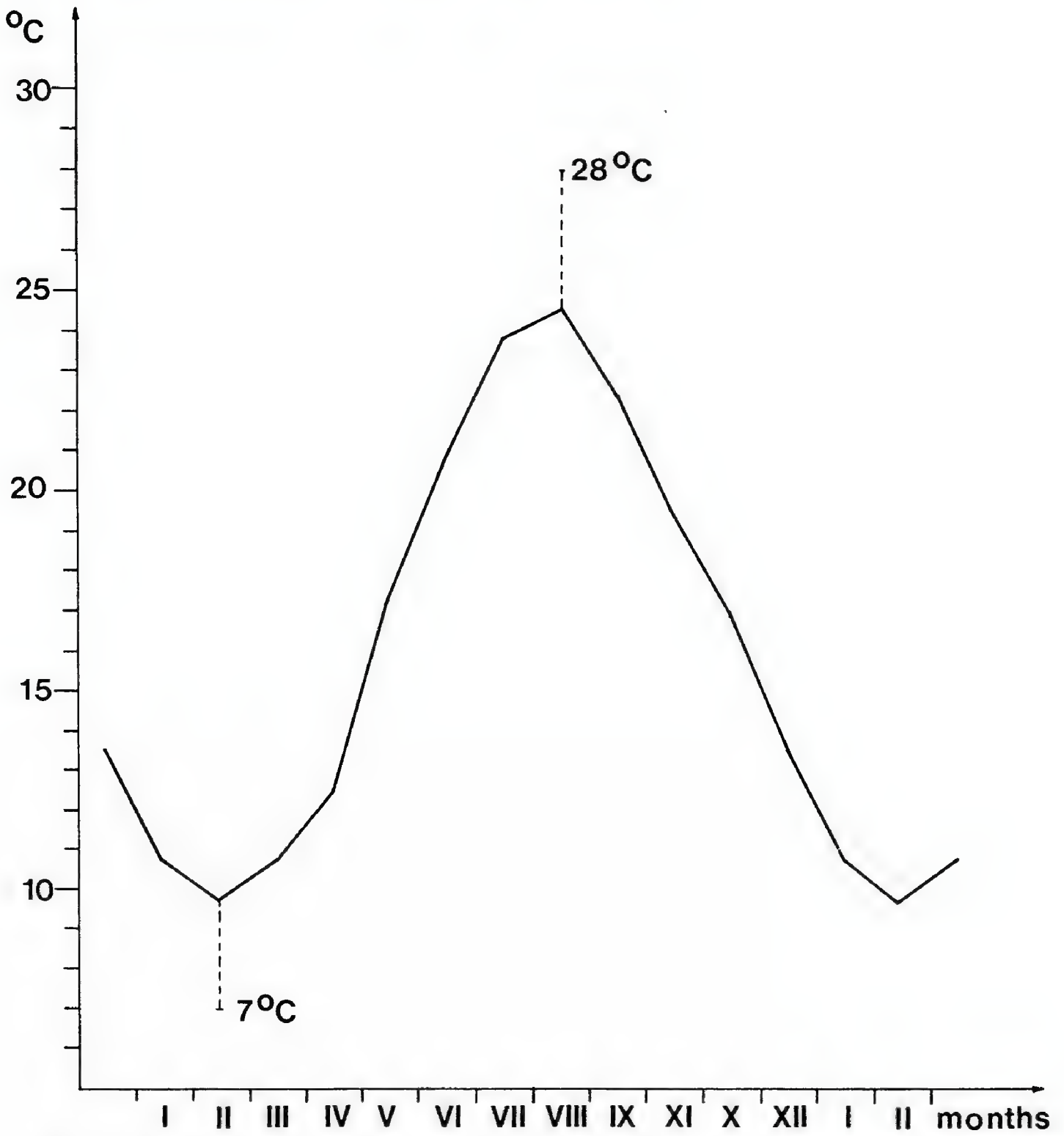


FIG. 1. Annual cycle of monthly mean sea surface temperatures in the northern Adriatic (data from Zore-Armanda 1968). Extremes (dashed lines) can reach 7°C in February and 28°C in August.

tion (Hutchison and Maness 1979, Reynolds and Casterlin 1979), which involves biochemical restructuring of the organism (Reynolds and Casterlin 1980). The range of temperatures over which an organism can acclimat(iz)e largely determines its eurythermality (Reynolds and Thomson 1974). Tropical marine reef fishes typically prefer water temperatures between 20° and 30°C (Reynolds and Casterlin 1981). They tend to be stressed by temperatures below about 12°C (Thomson and Lehner 1976). Typically, optimal temperatures for growth and other physiological functions are highly correlated with preferred temperatures (Jobling 1981, McCauley and Casselman 1981).

Some fishes thermoregulate behaviorally on a large scale by undertaking seasonal migrations in response to changing temperatures (Reynolds 1977). This response is exemplified not only by pelagic species, but also by demersal or benthic species such as the winter flounder *Pseudopleuronectes americanus*, which exhibits seasonal onshore-offshore migrations (Casterlin and Reynolds 1982). Thermal resource partitioning has been documented among temperate freshwater fishes (Magnuson *et al.*, 1979). However, comparatively little has been done to elucidate the thermal ecology of tropical reef fishes (Graham 1972, Thomson and Lehner 1976, Medvick and Miller 1979, Reynolds and Casterlin 1981).

Questions which we have sought to answer by field observations in the northern Adriatic are:

How do primary-resident reef fishes (*cf.* Thomson *et al.* 1979), partially of tropical affinities, respond to low winter water temperatures?

Do they migrate to deeper, warmer waters, or do they remain with their shallow sublittoral reef substrate?

If they remain, how is their behavioral ecology affected by the low temperatures?

Are niche shifts evident among different species with different thermal tolerances and optima, and if so, how are interspecific interactions altered as temperatures change seasonally?

The northern Adriatic provides an ideal outdoor "laboratory" for examining these questions because of the diversity of resident reef fishes subjected to such a wide range of annual changes in water temperature.

## Methods and Materials

Field observations were made by SCUBA diving at Banjole and Figarola Islands near Rovinj, Yugoslavia, between the hours of 0900 and 1600 local time daily, in February 1979, 1980 and 1981, January 1980, and April 1981. During each dive, water temperatures were measured from the surface to a depth of 10 m. The anaesthetic Quinaldine was used to capture small reef fishes for gut content analysis (*cf.* Table 1).

TABLE 1

Contents of stomachs and intestines of 6 *Scorpaena ustulata* captured with Quinaldine near mid-day during February. Blennies were distinguishable by their teeth.

| Total length (mm) | Sex | Stomach contents | Intestine contents | Collection Site | Collection Date |
|---|---|---|---|---|---|
| 139 | male | shrimps | *B. incognitus* | Figarola | 2/80 |
| 127 | female | empty | empty | Figarola | 2/80 |
| 141 | male | empty | polychaetes | Figarola | 2/80 |
| 170 | female | empty | crustaceans | Figarola | 2/81 |
| 150 | female | empty | crustaceans | Figarola | 2/81 |
| 158 | male | 1 *B. incognitus*<br>1 *Gobius* sp. | unidentified fish remains | Figarola | 2/81 |

## RESULTS AND DISCUSSION

The littoral tidepool blennies, *Blennius adriaticus* and *B. pavo* (Table 2), abandon the tidepools for subtidal waters in winter when the tidepool water

TABLE 2

Classification of, and some remarks concerning, important northern Adriatic reef fishes included in this study. (Note: 3 *Atherina* spp., pelagic planktivores occurring in large schools near shore, are not reef residents although they may often pass over reefs).

| Family | Species | Remarks |
|---|---|---|
| Pomacentridae (damselfishes) | *Chromis chromis* | the only Mediterranean sp.; planktivorous. |
| Labridae (wrasses) | | 10-11 spp. in N. Adriatic; mostly Aufwuchs-grazers with carnivorous tendencies. |
| | *Crenilabrus quinquemaculatus* | |
| | *C. pavo* | |
| | *Coris julis* | secondary reef resident. |
| Gobiidae (gobies) | | many spp. present. |
| | *Gobius cruentatus* | very common, large goby. |
| Scorpaenidae (scorpionfishes) | | 3 spp. in Mediterranean; important predators. |
| | *Scorpaena ustulata* | |
| Tripterygiidae (triplefin blennies) | | 3 spp. in N. Adriatic; benthic planktivores. |
| | *Tripterygion tripteronotus* | |
| Sparidae (porgies) | | 13 spp. in N. Adriatic; play ecological roles of acanthurids, siganids, lutjanids elsewhere. |
| | *Diplodus annularis* | |
| | *D. sargus* | |
| | *D. vulgaris* | |
| | *Oblada melanura* | only planktivore in group |
| Blenniidae (combtooth blennies) | | 15 spp. in N. Adriatic; primarily Aufwuchs-eaters, some with herbivorous or carnivorous preferences. |
| | *Blennius galerita* | |
| | *B. adriaticus* | inhabits tidepools. |
| | *B. pavo* | inhabits tidepools. |
| | *B. gattorugine* | |
| | *B. sanguinolentus* | |
| | *B. rouxi* | |
| | *B. incognitus* | |
| | *B. trigloides* | |

temperatures drop near 0°C on very cold nights. This avoidance of lethal temperatures constitutes a form of thermoregulatory behavior. However, the primary-resident reef fishes of the shallow (< 30 m) sublittoral region remain in their reef habitats throughout the year, even during periods of incapacitatingly low temperatures. In this regard it is important to note that below a depth of 30 m in the northern Adriatic there is a muddy-sandy bottom unsuitable for reef fishes. Thus, migration to depths below 30 m, where temperatures are slightly warmer in winter (about 12.5°C), is ecologically impractical for these reef residents.

Behavioral patterns and interspecific interactions change seasonally with water temperatures so that significant niche shifts occur among species with different evolutionary thermal histories. Species belonging to families with the most tropical affinities, such as the pomacentrid *Chromis chromis* (Table 2), become inactive and remain within the shelter of caves or crevices (Fig. 2) throughout the cold season. Other species which appear to be better

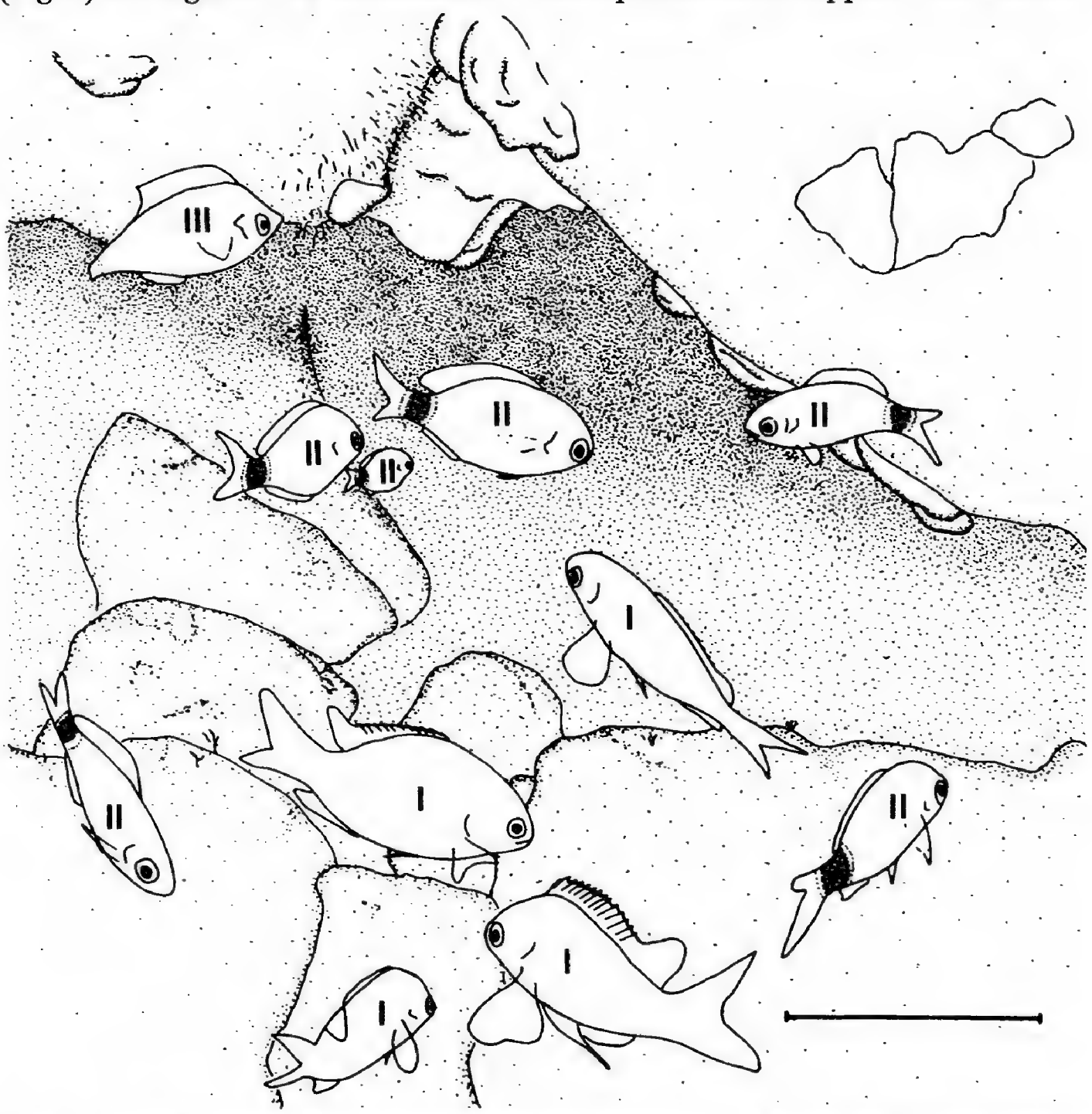


FIG. 2. Typical view of a mixed-species winter cave society, as seen from the entrance, in February 1980 (redrawn from a photograph). I, *Chromis chromis;* II, *Oblada melanura;* III, *Crenilabrus quinquemaculatus.* Bar in front indicates 10 cm.

adapted to cold, such as *Scorpaena ustulata,* feed opportunistically on other fishes (Table 1) incapacitated by the cold. During spring rewarming of the water, as observed in April, fishes react in a species-specific manner with a staggered enhancement of activity according to their thermal physiology (see below). Some species which are common in the southern Adriatic, such as *Anthias anthias, Apogon imberis,* and *Thalassoma pavo,* are lacking in similar habitats in the northern portion, presumably because of inability to tolerate the cold winter temperatures.

The most dramatic seasonal changes in behavioral ecology occur among the "suprademersal" species (*sensu* Abel 1961a)—those with gas bladders, which swim above the substrate when active but hide in reef caves or crevices when inactive. The normally facultative cave-dwellers become obligate cave-dwellers in the cold season and form dense mixed societies which remain within the shelter of caves (Fig. 2) throughout the winter. Predominant among this group are *Chromis chromis* and *Oblada melanura* (Fig. 2, Table 2). In winter, these fishes cannot be baited with opened sea urchins, which are normally an attractive food in summer. The distance between individuals in these mixed cave societies averages about 10 cm, and no inter- or intraspecific interactions are evident. Often these mixed winter cave societies are joined by *Diplodus annularis, D. sargus, D. vulgaris, Crenilabrus quinquemaculatus* and *C. pavo* (Table 2). On one occasion, even a school of *Boops* sp., which in summer never hide in caves, occurred there. *Coris julis* and *Seranella scriba,* secondary reef residents (*sensu* Thomson *et al.* 1979), were never seen in caves.

Among the benthic demersal species, which lack gas bladders and are almost always in contact with the substrate, the Aufwuchs-grazing Blenniidae and the benthic planktivorous Tripterygiidae were seldom visible on the substrate in February. Blennies and tripterygiids could be captured from comparable stretches of substrate by use of Quinaldine anaesthetic in both winter and summer. *Tripterygion tripteronotus,* which was never found in holes in the summer, remained in crevices at low winter temperatures. On a few occasions, free-sitting but inactive blennies (*Blennius galerita* and *B. gattorugine*) could be caught by hand, a feat impossible at higher temperatures. They showed a greatly diminished flight-distance. *B. sanguinolentus,* which flees at an approach distance of 2 m in summer, flees at 0.5 m in February. Only a single *B. rouxi* was seen in winter sitting free on the substrate; it was displaying the barred stress pattern (*cf.* Heymer and Zander 1978) instead of the typical black stripe on a white background seen at other times of the year. The blennies could not be baited by opened sea urchins, to which they are normally strongly attracted, but most of the blennies captured in winter nevertheless had full intestines (digestion may be slowed at low winter temperatures).

Predatory *Scorpaena ustulata* and *Gobius cruentatus* appeared to feed normally, and opportunistically, in February. *Scorpaena ustulata* were seen at about mid-day feeding on *Atherina* sp. (Large schools of *Atherina* appear denser and swim closer to the substrate in winter than in summer). *S.*

*ustulata* is, in summer, primarily a crepuscular predator, but it may benefit from the low sun angle and consequent low light intensity to feed at mid-day in winter, especially when their prey are affected by the cold. But contents (Table 1) of *S. ustulata* captured in winter revealed predation on blennies and gobies as well as on invertebrates. A *Gobius cruentatus* was observed in winter feeding upon a *Blennius incognitus.*

Observations in late April, at 13°C, indicate species-specific responses to rising water temperatures in spring. *C. chromis* remained in caves, and sparids were seldom seen free-swimming and never feeding. *C. chromis* does not spawn until July at water temperatures near 25°C (Abel 1961b). *T. tripteronotus* sat free upon the substrate, and males displayed in typical fashion (*cf.* Wirtz 1978). *Blennius gattorugine, B. sanguinolentus, B. galerita* and *B. trigloides* showed fully developed secondary sexual characteristics (Zander 1975), and fully ripe gonads. One female *B. sanguinolentus* caught immediately after spawning released eggs easily in response to mild pressure on the ventral region. *B. rouxi* showed markedly increased anal appendices, but was not observed to mate.

Most warm-water resident reef fishes remain inactive in shelter during winter. The wrasse *Coris julis* buries itself in loose sediment at temperatures below 14°C (Riedl 1970), as do many labrids prior to inactive periods or in response to danger. Small blennioid and gobioid fishes hide in crevices in both summer and winter; they exhibit little seasonal change. Suprademersal species that normally hide only when inactive in other seasons, hide both day and night in winter. The shelter-seeking response to cold likely is a deterrent to predation.

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## REFERENCES

ABEL, E. F. 1961a. Über die Beziehung mariner Fische zu Hartbodenstrukturen. *Sitzungsberichte der Osterreichischen Akademie der Wissenschaften.* 5:223–263.

_____. 1961b. Freiwasserstudien über das Fortpflanzungsverhalten des Mönchfisches *Chromis chromis* Linne, einem Vertreter der Pomacentriden im Mittelmeer. *Zeitschrift fuer Tierpsycologie.* 18:441–449.

CASTERLIN, M. E. and W. W. REYNOLDS. 1982. Thermoregulatory behavior and diel activity of yearling winter flounder, *Pseudopleuronectes americanus* (Walbaum). *Environmental Biology of Fishes.* 7:177–180.

GRAHAM, J. B. 1972. Low-temperature acclimation and the seasonal temperature sensitivity of some tropical marine fishes. *Physiological Zoology.* 45:1–13.

HEYMER, A. and C. D. ZANDER. 1978. Morphology and ecology of *Gobius vittatus* Vinciguerra 1883, and its possible mimicry relationship to *Blennius rouxi* Cocco 1833 in the Mediterranean. *Zeitschrift fuer Zoologische Systematik und Evolutionsforschung.* 16:132–143.

HUTCHISON, V. H. and J. D. MANESS. 1979. The role of behavior in temperature acclimation and tolerance in ectotherms. *American Zoologist.* 19:367–384.

JOBLING, M. 1981. Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. *Journal of Fish Biology.* 19:439–455.

MAGNUSON, J. J., L. B. CROWDER and P. A. MEDVICK. 1979. Temperature as an ecological resource. *American Zoologist.* **19**:331–343.

McCAULEY, R. W. and J. M. CASSELMAN. 1981. The final preferendum as an index of the temperature for optimum growth in fish, pp. 81–93. In Proc. World Symp. on Aquaculture in Heated Effluents and Recirculation Systems, Vol. 2. Heenemann-Verlag, Berlin.

MEDVICK, P. A. and J. M. MILLER. 1979. Behavioral thermoregulation in three Hawaiian reef fishes. *Environmental Biology of Fishes.* **4**:23–28.

REYNOLDS, W. W. 1977. Temperature as a proximate factor in orientation behavior. *Journal of the Fisheries Research Board of Canada.* **34**:734–739.

_____ (ed.). 1979. Thermoregulation in ectotherms. *American Zoologist.* **19**:191–384.

_____ and M. E. CASTERLIN. 1979. Behavioral thermoregulation and the "final preferendum" paradigm. *American Zoologist.* **19**:211–224.

_____ and _____. 1980. The role of temperature in the environmental physiology of fishes, pp. 497–518. In M.A. Ali, (ed.) Environmental Physiology of Fishes. NATO-ASI Series, Plenum, New York.

_____ and _____. 1981. Behavioral thermoregulatory abilities of tropical coral reef fishes: a comparison with temperate freshwater and marine fishes. *Environmental Biology of Fishes.* **6**:347–349.

_____ and D. A. THOMSON. 1974. Temperature and salinity tolerances of young Gulf of California grunion, *Leuresthes sardina* (Atheriniformes: Atherinidae). *Journal of Marine Research.* **32**:37–45.

RIEDL, R. (ed.). 1970. *Fauna und Flora der Adria.* Parey-Verlag, Berlin. 702 pp.

THOMSON, D. A., L. T. FINDLEY and A. N. KERSTITCH. 1979. *Reef Fishes of the Sea of Cortez—The Rocky Shore Fishes of the Gulf of California.* Wiley-Interscience, New York. 302 p.

_____ and C. E. LEHNER. 1976. Resilience of a rocky intertidal fish community in a physically unstable environment. *Journal of Experimental Marine Biology and Ecology.* **22**:1–29.

WIRTZ, P. 1978. The behaviour of the Mediterranean tripterygion species (Pisces, Blennioidea). *Zeitschrift fuer Tierpsycologie.* **48**:142–174.

ZANDER, C. D. 1975. Secondary sex characteristics of Blennioid fishes (Perciformes). *Pubblicazioni della Stazione Zoologica di Napoli.* **39**:717–727.

ZORE-ARMANDA, M. 1968. The system of currents in the Adriatic Sea. *Studies and Reviews. General Fisheries Council for the Mediterranean.* **34**:1–48.

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# OCEANOGRAPHY OF THE MISSISSIPPI RIVER BIGHT

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## EDITOR'S NOTE

The seven papers of this section have been assembled under the aegis of Dr. R. Eugene Turner of the Louisiana State University Center for Wetland Resources. These papers emphasize the nature and the importance of the various coastal and marine processes which are affected by the Mississippi River. The *Contributions in Marine Science* considers these papers to be of significance for their regional and practical values and for their general theoretical and academic values in related marine areas.

Donald E. Wohlschlag, *Editor*

# INTRODUCTORY REMARKS

The geographic location discussed in the seven papers that follow is the Northern Gulf of Mexico continental shelf, near the terminus of the Mississippi River. That river drains 27 states and 40% of the U.S., for which the drainage basin was properly called, "Body of the Nation" (*Life on the Mississippi,* Ch. 1, Mark Twain). It is the largest river in the U.S. by any criteria, including geomorphology and content. Within it are large portions of the nation's garbage, industrial remnants, nutrients, excellent soils, and flora and fauna. The river passes through the American equivalent of the industrialized Ruhr Valley and two of the five largest harbor ports in the U.S. The coast line it built over seven thousand years contains 45% of the U.S. coastal wetlands. Just offshore, amidst extensive oil and gas recovery operations, are harvested 30% of the U.S. annual fisheries landings. It is a remarkable river also for its influence on a continental shelf that we are only just now beginning to study diligently.

Aspects of these river-ocean interactions are conspicuously evident in these papers. Vertical stratification of the water column near the river mouth leads to the isolation of water masses and reduced mixing. Horizontal freshwater diffusion varies with changes in meteorological forcing functions, which result in distinctive biological communities and dilution rates. River sediment transport, as well as the lack of transport, affects community composition and metabolism and also subsurface water characteristics. The location of the river plume may change, but it is hoped that the basic physical phenomena taking place within it are coupled in time and space and are therefore always observable. If a worthwhile goal is to understand how the system "works," then we must admit that it is too complex an area for study in the isolation of one discipline. For that reason alone it seems justifiable to gather these diverse papers together in *Contributions in Marine Science.* We thank the editor for the opportunity to do so.

R. Eugene Turner
*Center for Wetland Resources*
*Louisiana State University*
*Baton Rouge, Louisiana*

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# TEMPERATURE AND SALINITY VARIABILITY WITHIN THE LOUISIANA BIGHT

Wm. J. Wiseman, Jr., S. P. Murray, J. M. Bane[1], and M. W. Tubman[2]

*Coastal Studies Institute, Louisiana State University, Baton Rouge, Louisiana 70803*

## ABSTRACT

Waters from three different sources, with identifiable temperature and salinity characteristics, appear to mix locally to form the waters of the Louisiana Bight. The seasonal variations of the characteristics of these source waters are described and related to meteorological and riverine forcing. Strong stratification caused by Mississippi River runoff isolates the surface layers from the deeper waters and the latter from air-sea interaction. Winter cold fronts force internal near-inertial oscillations, which affect the breakdown of the Mississippi River plume.

## INTRODUCTION

Recent progress in understanding Mississippi River near-field effluent plumes (Wright and Coleman 1971, Wiseman *et al.* 1976c) has not been accompanied by a similar understanding of those processes controlling the far-field plume interaction with ambient shelf waters. The purpose of this paper is to characterize the hydrography of the inner continental shelf immediately west of Southwest Pass, the Louisiana Bight, and the interactions of freshwater discharge with physical processes affecting that hydrography. The area to be described is bounded by the Mississippi River delta on the east and a north-south line at longitude 90°13′W on the west. The majority of our data, collected between June 1973 and April 1974 (Wiseman *et al.* 1976b), lies north of 28°50′N (Fig. 1).

Perret *et al.* (1971) calculate the annual mean discharge of the Mississippi River at $13.5 \times 10^3$ m$^3$ s$^{-1}$. Of the total discharge from the Mississippi River, 30% empties through Southwest Pass to affect directly the study area. This is further augmented by drainage through minor passes and crevasses. During the 1973 flood, the largest in recorded history, the annual mean discharge was $27.7 \times 10^3$ m$^3$ s$^{-1}$ (U.S. Army Corps of Engineers, unpublished data). Another strong flood occurred in 1974. Thus, our observations may be more representative of high flood years than of normal years. We do not, though, believe that this alters the basic conclusions concerning the processes active in the region.

[1]Marine Sciences Program and Department of Physics, University of North Carolina, Chapel Hill, North Carolina 27515

[2]1 West Coast Terrace, Hong Leong Garden, Singapore 0512.

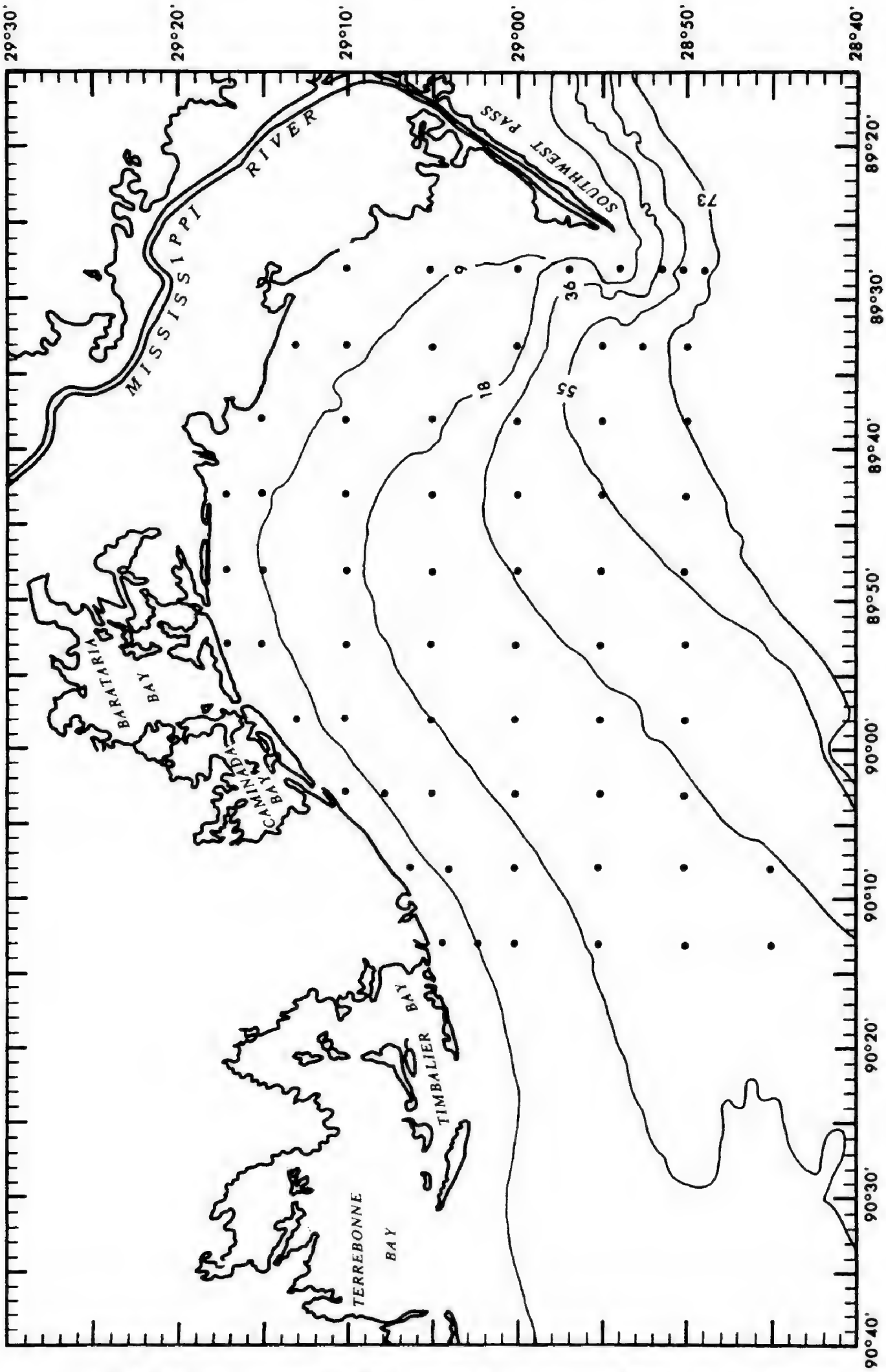


FIG. 1. Chart of the Louisiana Bight showing the sampling grid for the 1973–1974 hydrographic surveys. Depths are in meters.

## METEOROLOGICAL ENVIRONMENT

Large-scale atmospheric circulation over the northern Gulf of Mexico is dominated by the Bermuda-Azores High Pressure Cell. During summer the cell is well developed in a southerly position, causing predominantly light southeasterly winds. As summer progresses to fall, winds generally increase in speed and shift to a more easterly and northeasterly direction (Orton 1964). Winter brings higher wind speeds and directions that are the most variable of the year (Orton 1964). Spring is a period of transition. A notable lack of westerly wind components is apparent throughout the year. Both September and October represent times of peak tropical storm and hurricane activity, although such storms may occur from June through November (U.S. Weather Bureau 1959).

During winter months, cold fronts, or "northers," bring strong north and northwest winds into the area. The passage of these fronts strongly influences the near-surface currents in the tidal-inertial frequency range (Daddio 1977). Fifteen or twenty such passages are expected each winter (Leipper 1954). From March through May, the fronts tend to stall north of the coast and to become less frequent.

## HYDROGRAPHY

The salinity and temperature fields were mapped monthly on eight 3-day cruises between July 1973 and April 1974, except for December 1973 and March 1974. Station spacing was approximately 9 km (Fig. 1), although bad weather occasionally reduced the number of stations sampled. Significant month-to-month variations were observed in the data.

During the year, water temperatures range from greater than 31°C to less than 8°C, and salinities range from greater than 36‰ to nearly 0‰. Waters at the depths being considered lie within the surface layer (Nowlin 1971, 1972). The quoted variability in their characteristics would normally be attributed to intense air-sea interaction and runoff. If, though, one plots all water sample characteristics from a single monthly cruise as a scatter plot on a t–s diagram, the points for any month generally fall along two intersecting straight lines (Fig. 2). This suggests that locally, in both time and space, the waters within the Bight might be considered as resulting from the mixing of water from three sources, each of very homogeneous characteristics. (We will refrain from calling these "water types," as that term seems to have a somewhat narrower definition, although at any instant in time the sources behave, locally, much like water types.)

One source is low-salinity water derived predominantly from Southwest Pass effluent, but augmented by effluent from other local crevasses, bayous, and estuaries. The temperature of this light surface layer varies over a broad range during the course of a year, due both to local air-sea interaction and to variations in river water temperature.

A second source is cold and saline. Its salinity is always well above 36‰. It is the densest water found in the Bight. The local influence of this water

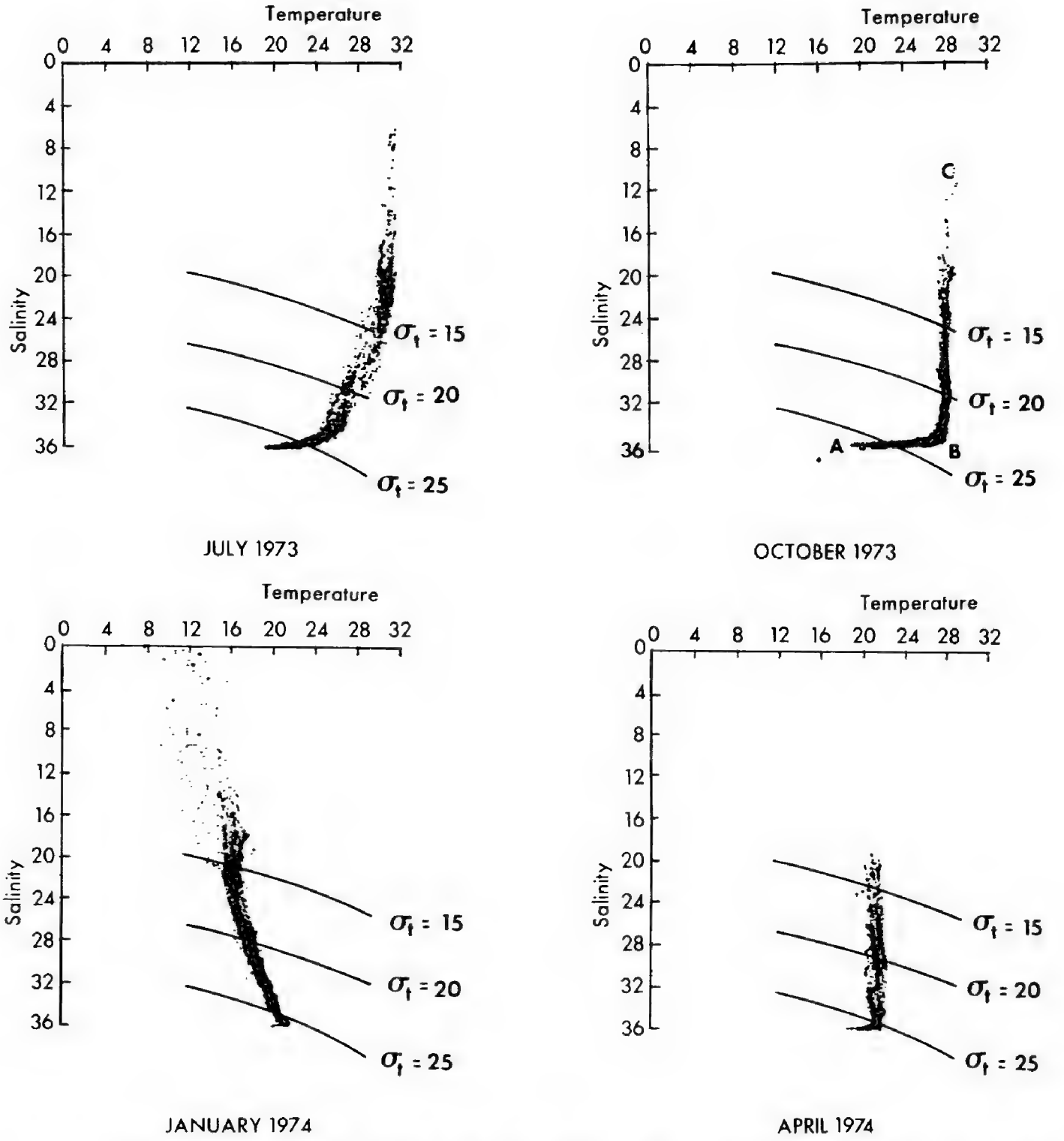


FIG. 2. Temperature-salinity scatter plots for data taken during the cruises in July 1973 (upper left), October 1973 (upper right), January 1974 (lower left), and April 1974 (lower right). The three source waters are indicated on the upper right panel by capital letters: cold, salty source (A), warm, salty source (B), and low-salinity source (C).

source on the study area appears seasonal in the 1973–74 data. It begins to intrude onto the inner shelf in later winter/early spring and has its greatest extent in mid-summer. By mid-fall it has retreated from the study area. A similar cycle was present in 1975 (Allen *et al.* 1977; Allen and Turner 1977a, b). Data from 1963–1965 (Temple *et al.* 1977) show no consistent evidence of such an intrusion of salty bottom water during the summer months. The vertical resolution of these data, though, was less than the data from the mid-1970s. The 1963–1965 data do confirm the presence of three source waters within the Bight, but the heaviest water is slightly less salty than the

warmer overlying water in this data set. This is in contrast to the later data set, where the heaviest water is also the saltiest.

The third source water has higher salinities than the first and higher temperatures than the second. In general, its temperature varies seasonally; it lags behind the pattern of the low-salinity water's thermal variation and undergoes less extreme changes.

Although the clearest pattern appearing on these t-s diagrams is one of two intersecting straight lines, some curvature does occasionally appear in the plots, *e.g.*, the July and January data (Fig. 2). This curvature could be due to 1) a rapid change in the characteristics of one of the source waters (Loder and Reichard 1981), 2) intensification of the local mixing processes, or 3) a longer residence time within the Bight for water from the warm, saline source. All three possibilities seem reasonable and are probably important at different times.

The large discharge of low-salinity water from Southwest Pass makes surface salinity an excellent tracer for water motion in this area. Maps of sea surface salinity (*e.g.*, Fig. 3) often indicate a plume of water extending westward from Southwest Pass and recurving anticyclonically into the study area. This pattern, which appears to be present approximately two-thirds of the time, has also been observed on LANDSAT images (Rouse and Coleman 1976, Wiseman *et al.* 1976a) and is further supported by drift card returns and drogue tracks. Rouse and Coleman (1976) state that plume morphology is controlled by Mississippi River stage and local wind stress. Surface currents within the plume flow parallel to the isohalines. Thus, to the extent that plume position is wind controlled, so are the surface currents. Lateral dispersion of the waters from the plume as well as from other minor coastal sources of low-salinity water forms a cap of low-salinity water over the entire region. This surface layer is separated from the underlying water by a very stable halocline (*e.g.*, Fig. 4).

Cross-shelf sections of salinity and temperature show strong, omnipresent haline stratification and much weaker thermal stratification. The latter is even destablizing in winter. During winter a lower layer of warm inner-shelf water is trapped between cooler waters both above and offshore (Fig. 5). The isopycnal slopes within this layer suggest a westward flow along the shelf. Data collected by Allen *et al.* (1977) show such a structure both east and west of the delta, with some indication of a connection between the two.

Although there is a large seasonal variability in the temperature-salinity characteristics of the waters of the Bight, in all seasons and throughout the region we find significant fine structure (Fig. 4). The step structure is believed to result from the breakdown of the far-field Mississippi River plume (Wiseman *et al.* 1976a).

## DISCUSSION

The waters of the Louisiana Bight may be considered as having three sources. The heaviest of these is a cold, high-salinity water which has been

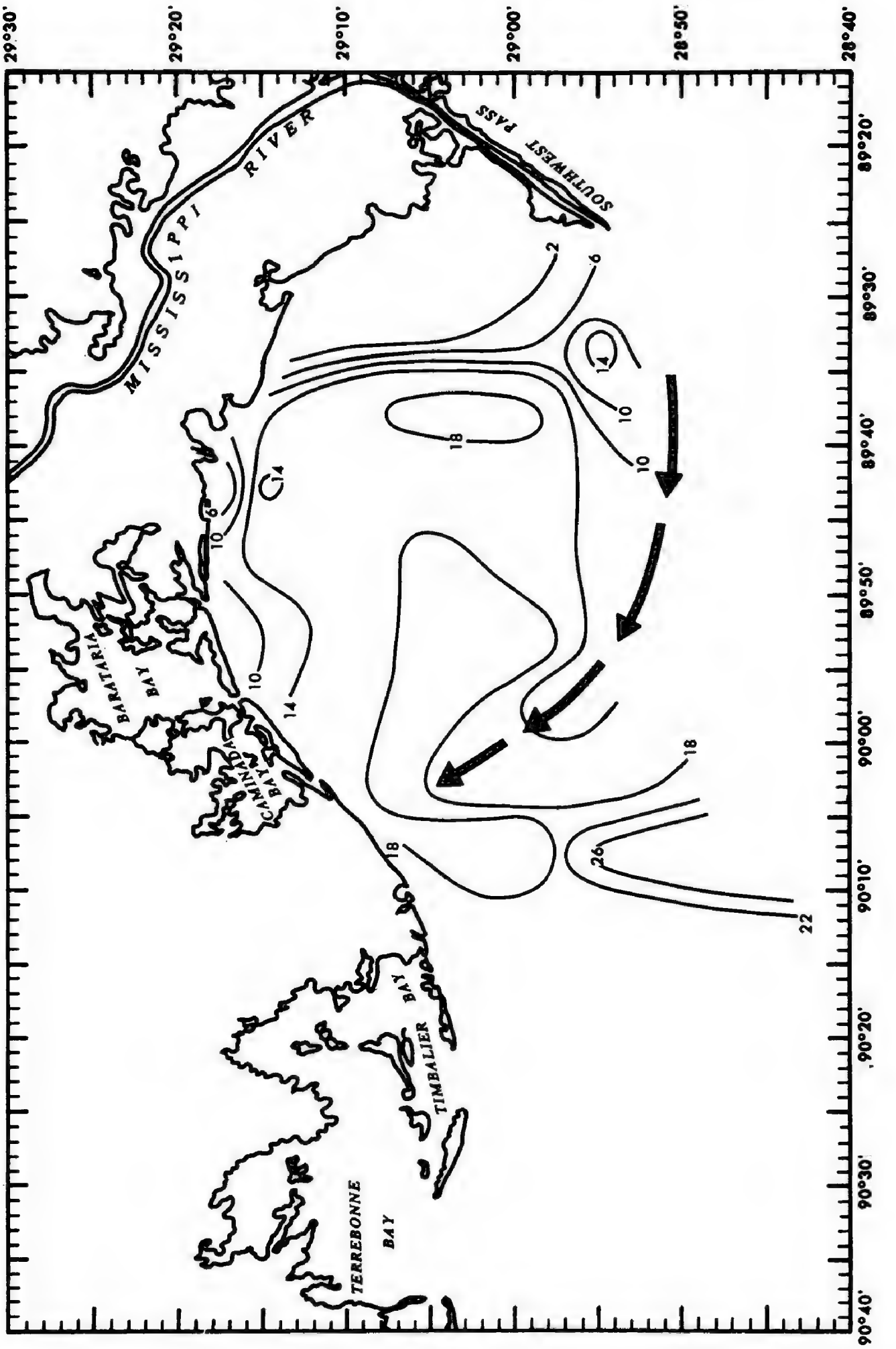


FIG. 3. Map of sea surface salinity drawn from the January 1974 data. The flow of the low-salinity plume from Southwest Pass is indicated by bold arrows.

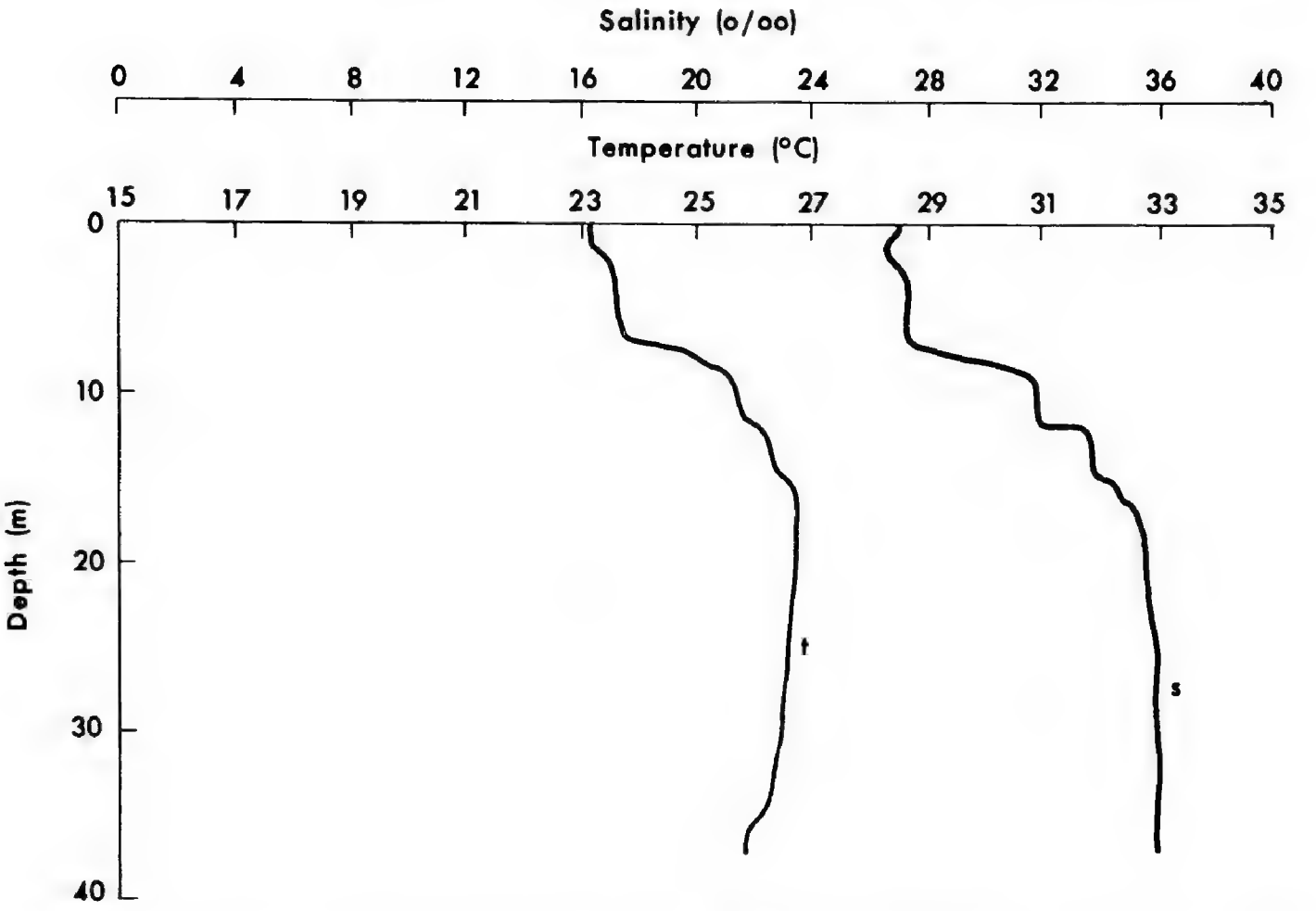


FIG. 4. Temperature and salinity profiles from 28°58.5′N, 89°34.3′W, on 29 October 1973. Note the strong halocline at about 8 m depth and the temperature and salinity steps beneath it.

observed to intrude onto the inner shelf in spring and retreat offshore in fall. The cause of this cycle, though, is unknown. It may be a response to local wind shifts or changes in Mississippi River discharge, or it may be part of a larger, Gulf-wide seasonal pattern (Sturges and Blaha 1976, Blaha and Sturges 1981). The source with intermediate density, a water of moderately high salinity and seasonally varying temperature, has an unknown origin. The presence of the third source, though, low-salinity water originating with the effluent from the Mississippi River system, appears to influence strongly the local thermal variations of the warm, saline waters.

The strong halocline occurring at the base of the low-salinity surface layer isolates the deeper waters from the effects of air-sea interaction. Only fresh surface waters are cooled by northers and mixed by convective overturning. Farther offshore, haline stratification is less intense. Cooling and wind mixing as the northers pass can thus propagate to greater depths than is possible closer to shore. The net result is to leave a pool of warm water at depth over the inner shelf. Isopycnal slopes within this pool indicate a westward drift, which suggests that the slow temporal changes observed in these waters during winter may be due to westward advection of thermal signals generated by air-sea interaction farther east.

While the intermediate-depth waters of the Bight are isolated from the atmosphere, the low-salinity surface layer is not. The dominant control on temperature of the surface layers of the Bight during winter is air-sea

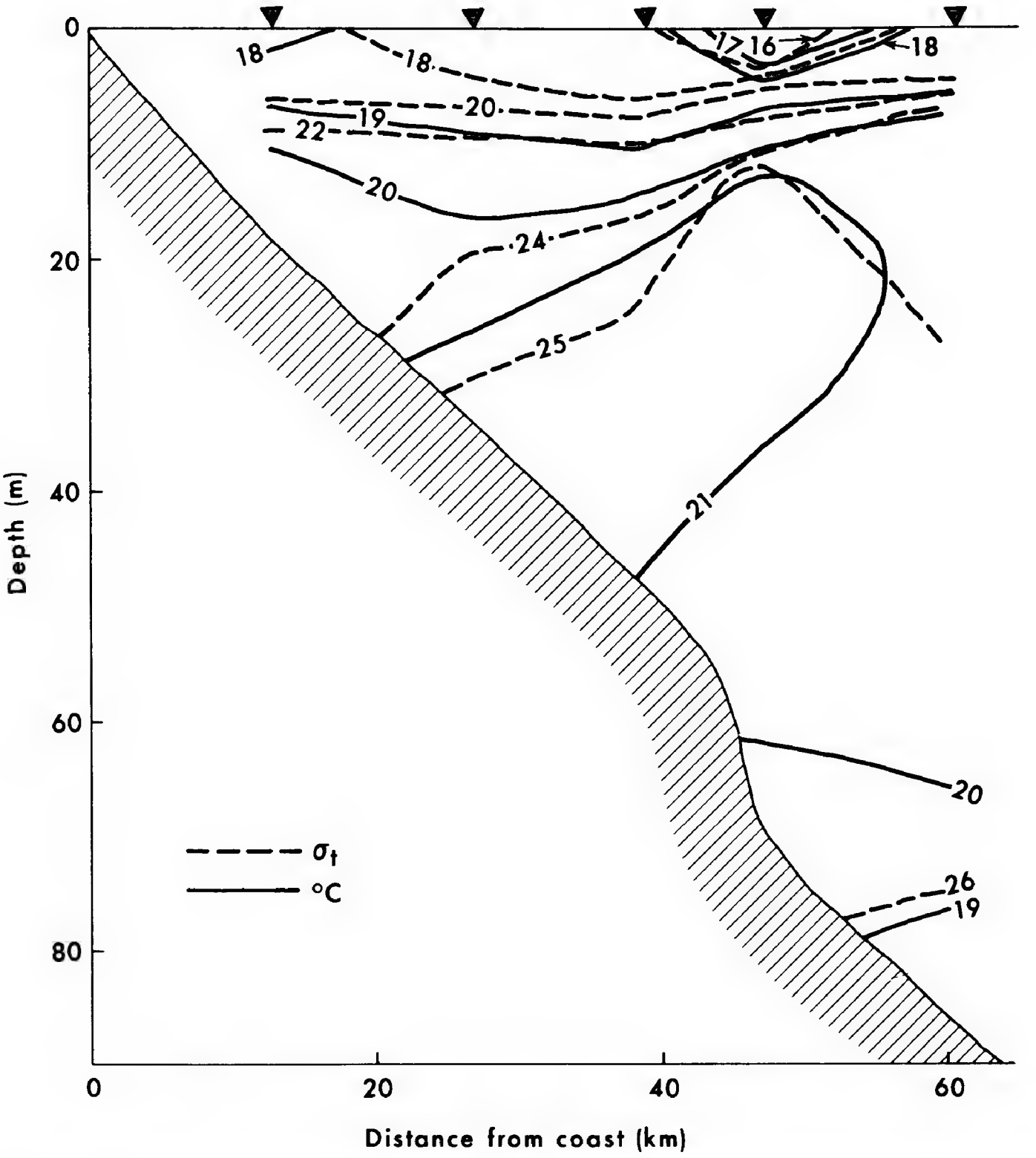


FIG. 5. Temperature and sigma-t cross-section along a line running approximately southeast from Caminada Bay perpendicular to the bottom contours. The data were taken in March 1975 (Allen *et al.*, 1977). Note the warm (21°) water trapped over the inner shelf and the strong pycnocline (halocline) in the surface layers.

interaction during frontal passages. When the northers pass over the area, there is strong heat loss from the surface waters, both latent and sensible (Nowlin and Parker 1974). The cooling of these waters occurs sporadically in time (Nowlin 1972) and forms multiple sea-surface temperature fronts in the offshore direction (Huh *et al.* 1978).

Along most continental shelves, surface wind stress is a dominant forcing mechanism for subtidal circulation (Winant 1980). As mentioned above,

within the Bight wind may partially control the near-surface flow (Rouse and Coleman 1976), but in such a highly stratified situation the waters below the halocline are probably driven by only the most persistent winds (Chuang *et al.* 1982), or the strongest. Tropical Storm Delia passed through the study area in September 1973. This event homogenized the water column, but the pre-storm stratified situation had returned by the time of our next cruise, 2 weeks later. Thus, even such intense events have only short-lived effects on the local hydrography.

Tropical storms and hurricanes, even along the Louisiana coast, are relatively uncommon events. The strong winter cold front passages are far more common. Because of their brief duration, their influence on the stratified water column of the Louisiana Bight, apart from the cooling mentioned above, is primarily the generation of near-inertial oscillations and deepening of the mixed layer.

Daddio (1977) first noted that the water motion at diurnal frequencies often bore no obvious relation to the tidal stage. Later, time series analysis showed that the amplitude of the motion increased substantially following cold front passages and decayed with a time scale of about 2 days (Daddio *et al.* 1978). Daddio *et al.* (1978) successfully modeled the observed currents using an inertial current model (Pollard and Millard 1970). Wiseman *et al.* (1978) argue that the apparent success of the model in reproducing Louisiana Bight currents was fortuitous and that, in fact, what occurs is not local forcing of the inertial oscillations but propagation of the disturbance from the coast. Strong southerly winds which precede a cold front pile up water against the coast. As the winds shift during the frontal passage and the stress relaxes, the halocline, which has been depressed at the coast, rebounds, and internal, near-inertial waves propagate outward from the coast. These waves propagate predominantly along the halocline, but also, because they are not precisely at the inertial frequency, vertically within the stratified water beneath the halocline. Thus, they may transport momentum out of the surface layer.

We believe that the fine structure observed in the Bight and mentioned above is the result of the processes responsible for the breakdown of the far-field river plume. We have suggested that one important process might be the instability of packets of high-frequency internal waves in the shear of the internal tide (Wiseman *et al.* 1976a). Similar instability may occur in the shear, at the base of the mixed layer, associated with the near-inertial oscillations just described. One further process for generating fine structure is also related to frontal passages. The deepening of the mixed layer during a frontal passage is a function of the strength of the winds during the frontal passage and the density difference developed between the surface waters and the underlying waters because of river discharge during the time between frontal passages. Since both factors are random processes, the extent of mixed-layer deepening by any given frontal passage is random. A sequence of frontal passages may thus generate a layered water structure. It should be remembered that, while the fine structure was observed in all

seasons, strong fronts are restricted to the period between midautumn and midspring. Frontal effects, therefore, cannot totally explain the observed fine structure.

In a region with such strong vertical stratification in both temperature and salinity, double diffusive phenomena might be suspected of causing step structures. The signs of the gradients necessary for double diffusion phenomena occur only during the winter months, yet we find fine structure in the water column throughout the year. This process, then, cannot explain all the fine structure. Furthermore, many of the situations observed in winter lie in the stable region of the Rayleigh Number diagram (Turner 1973, Fig. 8.2), which suggests that the stratification is stable to double diffusive phenomena. Thus, while double diffusion cannot be categorically stated to be absent from the region, it does not appear to be a significant process at the scales we are discussing.

## CONCLUDING REMARKS

The massive amount of effluent discharged by Southwest Pass into the Louisiana Bight significantly influences the hydrography of the area. It directly forces a large seasonal cycle in salinity and makes the surface waters more responsive to air-sea interaction than might be expected in waters of comparable depth. Furthermore, it isolates the underlying waters from such air-sea interactions, thus restricting the variability of these waters. What is not clear is how far west such an influence is felt along the shelf. Low-salinity water can be traced westward from the Mississippi River delta along the shelf to the Texas-Mexico border. Effluent from the Atchafalaya River reinforces this signal near 91°15′W. The seasonal signal forced by the spring flood of these two rivers can be seen in the salinities of the Texas shelf with about a 1-month lag (Temple *et al.* 1977, NOAA 1976). The fine structure, so prevalent near the Mississippi River delta, though, is absent along the Texas shelf. Cold front passages over the Texas shelf are quite capable of mixing shelf waters to the bottom and severely altering their local temperature and salinity characteristics (Nowlin and Parker 1976), possibly to the point of forming intermediate water for the western Gulf. Clearly the processes affecting the shelf waters this far west are significantly different from those controlling the waters of the Louisiana Bight.

## ACKNOWLEDGMENTS

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## REFERENCES

ALLEN, R. L. and R. E. TURNER. 1977a. Mississippi delta bight studies, No. 2, Hydrographic data: July 15–24, 1975. Center for Wetland Resources, Louisiana State Univ., Baton Rouge, LA, 71 pp.

_____ and _____. 1977b. Mississippi delta bight studies, No. 3, Hydrographic data: October 28–November 7, 1975. Center for Wetland Resources, Louisiana State Univ., Baton Rouge, LA, 47 pp.

_____, _____ and L. J. ROUSE. 1977. Mississippi delta bight studies No. 1, Hydrographic data: March 11–27, 1975. Center for Wetland Resources, Louisiana State Univ., Baton Rouge, LA, 87 pp.

BLAHA, J. P. and W. STURGES. 1981. Evidence for wind-forced circulation in the Gulf of Mexico. *Journal of Marine Research.* 39(4):711–734.

CHUANG, W.-S., W. W. SCHROEDER and WM. J. WISEMAN, JR. 1982. Summer current observations off the Alabama Coast. *Contributions in Marine Science.* 25:121–131.

DADDIO, ERNEST. 1977. Response of coastal waters to atmospheric frontal passage in the Mississippi Delta region. Tech. Rept. 234, Coastal Studies Inst., Louisiana State Univ., Baton Rouge, 38 pp.

_____, WM. J. WISEMAN, JR. and S. P. MURRAY. 1978. Inertial currents over the inner shelf near 30°N. *Journal of Physical Oceanography.* 8(4):728–733.

HUH, O. K., WM. J. WISEMAN, JR. and L. J. ROUSE, JR. 1978. Winter cycle of sea surface thermal patterns, northeastern Gulf of Mexico. *Journal of Geophysical Research.* 83(C9):4523–4529.

LEIPPER, D. F. 1954. Marine meteorology of the Gulf of Mexico. *Fishery Bulletin.* 55(86):89–98.

LODER, T. C. and R. P. REICHARD. 1981. The dynamics of conservative mixing in estuaries. *Estuaries.* 4(1):64–69.

NOAA. 1976. Environmental studies of the south Texas outer continental shelf 1975, vol. II, Physical oceanography. 290 pp.

NOWLIN, W. D., JR. 1971. Water masses and general circulation of the Gulf of Mexico. *Oceanology International and Offshore Technology.* 6(2):28–33.

_____. 1972. Winter circulation patterns and property distributions. In L. R. A. Capurro and J. L. Reid (eds.) *Contributions on the Physical Oceanography of the Gulf of Mexico,* vol. 2. Texas A and M Univ., Oceanographic Studies. Gulf Publishing Co., Houston.

_____ and C. A. PARKER. 1974. Effects of a cold-air outbreak on shelf waters of the Gulf of Mexico. *Journal of Physical Oceanography.* 4(3):467–486.

ORTON, R. B. 1964. The climate of Texas and the adjacent Gulf waters. U.S. Weather Bureau, Washington, D.C.

PERRET, W. S., B. B. BARRETT, W. R. LATAPIE, J. F. POLLARD, W. R. MOCK, G. B. ADKINS, W. J. GAIDRY and C. J. WHITE. 1971. *Cooperative Gulf of Mexico estuarine inventory and study, Louisiana. Phase I, Area Description.* Louisiana Wild Life and Fisheries Commission, New Orleans, LA.

POLLARD, R. T. and R. C. MILLARD. 1970. Comparison between observed and simulated wind-generated inertial oscillations. *Deep-Sea Research.* 17:813–821.

ROUSE, L. J. and J. M. COLEMAN. 1976. Circulation observations in the Louisiana Bight using LANDSAT imagery. *Remote Sensing of Environment.* 5:55–66.

STURGES, W. and J. P. BLAHA. 1976. A western boundary current in the Gulf of Mexico. *Science.* 192:367–369.

TEMPLE, R. F., D. L. HARRINGTON and J. A. MARTIN. 1977. Monthly temperature and salinity measurements of continental shelf waters of the northwestern Gulf of Mexico, 1963–65. *NOAA Technical Report NMFS, SSRF* 707. 26pp.

TURNER, J. S. 1973. *Buoyancy effects in fluids.* Cambridge Univ. Press, 367 pp.

U.S. WEATHER BUREAU. 1959. Climatological and oceanographic atlas for mariners, vol. 1, North Atlantic Ocean.

WINANT, C. D. 1980. Coastal circulation and wind-induced currents. In M. van Dyke, J. V. Wehausen and J. L. Lumley (eds.) *Annual Review of Fluid Mechanics,* vol. 12.

WISEMAN, WM. J., JR., J. M. BANE, S. P. MURRAY and M. W. TUBMAN. 1976a. Small-scale temperature and salinity structure over the inner shelf west of the Mississippi River delta. *Memoires de la Societe Royale des Sciences de Liege.* 6(x):277–285.

_____, S. P. MURRAY, J. M. BANE and M. W. TUBMAN. 1976b. Offshore physical oceanography. In J. G. Gosselink, R. R. Miller, M. Hood and L. M. Bahr, Jr., (eds.) *Louisiana Offshore Oil Port: Environmental Baseline Study.* LOOP, Inc., New Orleans, LA.

_____, L. J. ROUSE, JR. and O. K. HUH. 1978. Mixed layer models for coastal waters. 3:2619–2632. *Proceedings, 16th Coastal Engineering Conference,* Hamburg, Germany.

_____, L. D. WRIGHT, L. J. ROUSE and J. M. COLEMAN. 1976c. Periodic phenomena at the mouth of the Mississippi River. *Contributions in Marine Science.* **20**:11–32.

WRIGHT, L. D. and J. M. COLEMAN. 1971. Effluent expansion and interfacial mixing in the presence of a salt wedge, Mississippi River delta. *Journal of Geophysical Research.* **76**(36):8649–8661.

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# SUMMER CURRENT OBSERVATIONS OFF THE ALABAMA COAST[1]

Wen-Ssn Chuang, William W. Schroeder[2], and Wm. J. Wiseman, Jr.

Coastal Studies Institute, Louisiana State University,
Baton Rouge, Louisiana 70803

## ABSTRACT

Low-frequency current variability on the Alabama shelf is examined from three years (1976, 1978, and 1979) of summer current, sea level, and meteorological records. The analysis shows that the shelf water response to local wind forcing is frequency dependent; alongshore current and sea level are driven by the alongshore wind at time scales longer than a week, but they are generally not correlated at shorter periods. Since the mean wind varies between the three study seasons, a permanent summer circulation pattern does not exist. The variations in frequency response also indicate that circulation is strongly affected by the wind duration, density stratification, and coastal geometry.

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## INTRODUCTION

Studies of shelf circulation in the northern Gulf of Mexico are limited. Most direct current measurements have been made near the central Texas coast (Smith 1978, 1979). These data indicate that subtidal current fluctuations in the alongshore direction are coherent throughout the water column, and are driven by the alongshore wind. In the cross-shelf direction, the current is less organized, but an onshore or offshore mass flux often occurs at all levels simultaneously. This phenomenon can be explained by alongshore variations in the flow field. Smith (1980) demonstrated that the alongshore current speed can be quite different between two stations with an alongshore separation of 120 km.

In the region east of the Mississippi Delta, only the most rudimentary, and often conflicting, information is available. Also, most of this information relates solely to the surface circulation. Leipper (1954) presents surface flow patterns based on pilot charts. He suggests an easterly flow over the outer shelf in June, which is, presumably, associated with the Loop Current. In

[1]Contribution No. 45 of the Marine Environmental Sciences Consortium and Contribution No. 44 of the Aquatic Biology Program of the University of Alabama

[2]Address: Marine Sciences Program, The University of Alabama, Dauphin Island, Alabama 36528

December, he indicates a closed cyclonic circulation between the Mississippi Delta and Cape San Blas, Florida, with the easterly flow over the slope. Drennan (1968) interprets surface temperature and salinity patterns in terms of a similar cyclonic flow regime. He stresses the topographic steering effect of the DeSoto Canyon in turning a semi-permanent easterly current shoreward, and effects of both vertical and lateral drag in forming the inferred cyclonic gyre. However, any hypothesized shelf regime that depends on a seasonal easterly flow over the continental slope driven by Loop Current intrusions cannot be supported by recent observational and theoretical studies (e.g., Vukovich *et al.* 1979; Hurlburt and Thompson 1980), as these studies suggest that northward intrusions are aperiodic, or at least not tied to an annual cycle.

The only available current profiles from this region are a short data set east of the Mississippi Delta collected by Murray (1972). After a tidal current of approximately 15 cm $s^{-1}$ is removed, the influence of wind and horizontal density gradients becomes evident: a strong onshore wind results in a transient two-layer flow in the cross-shelf direction. On the other hand, after the wind has persisted for 3 days, a relatively stable flow pattern is established. The record, however, is too short to estimate reliably a mean current.

In the present study, the summer current variation near the Alabama coast and its relation to wind forcing is examined for three different years (1976, 1978, and 1979). The duration of the records varies from 70 to 90 days, which enables us to resolve long-period fluctuations of up to 20 days, as well as to estimate the year-to-year change in the summer mean flow. Simultaneously collected sea level data at a nearby coastal station are also included in the analysis.

## OBSERVATIONS

The current meter mooring (30°01′N, 88°05′W) was located 26 km south of Dauphin Island in water 25 m deep (Fig. 1). An ENDECO Type 105 current meter (set at 1-hour sampling interval) was placed 5 m above the bottom from June to August (or early September) in the three study years. This meter measures speed with an accuracy of 2.7 cm $s^{-1}$ per hourly sample and direction with an accuracy of 7° per hourly sample.

The coastline runs approximately east-west, which is taken as the alongshore direction. In the vicinity of the mooring the shelf is broad and relatively flat (the offshore bottom gradients are generally less than 1 m/1000 m); the shelf break lies about 85 km to the south. West of 88°W longitude the isobaths first trend east-west, then turn abruptly north-south at the Chandeleur Islands (about 50 km away from the mooring site). To the east, the isobaths are extremely convoluted (details are not shown in Fig. 1), but all converge to an ENE–WSW direction along the edge of DeSoto Canyon.

During the summer months the shelf waters are both thermally and haline stratified. The strongest pycnocline development is usually found between 5- and 10-m depth. Surface to bottom temperature and salinity differences of up to 10°C and 10‰ have been observed (Schroeder and Crozier 1974; Thompson and Leming 1978). Much of the haline stratification can be attributed to the large but highly seasonal freshwater runoff to this region. Four rivers account for most of the runoff: the Mobile, the Pascagoula, the Pearl, and the Mississippi. The last carries, by far, the greatest discharge, but it also lies farthest from the mooring site.

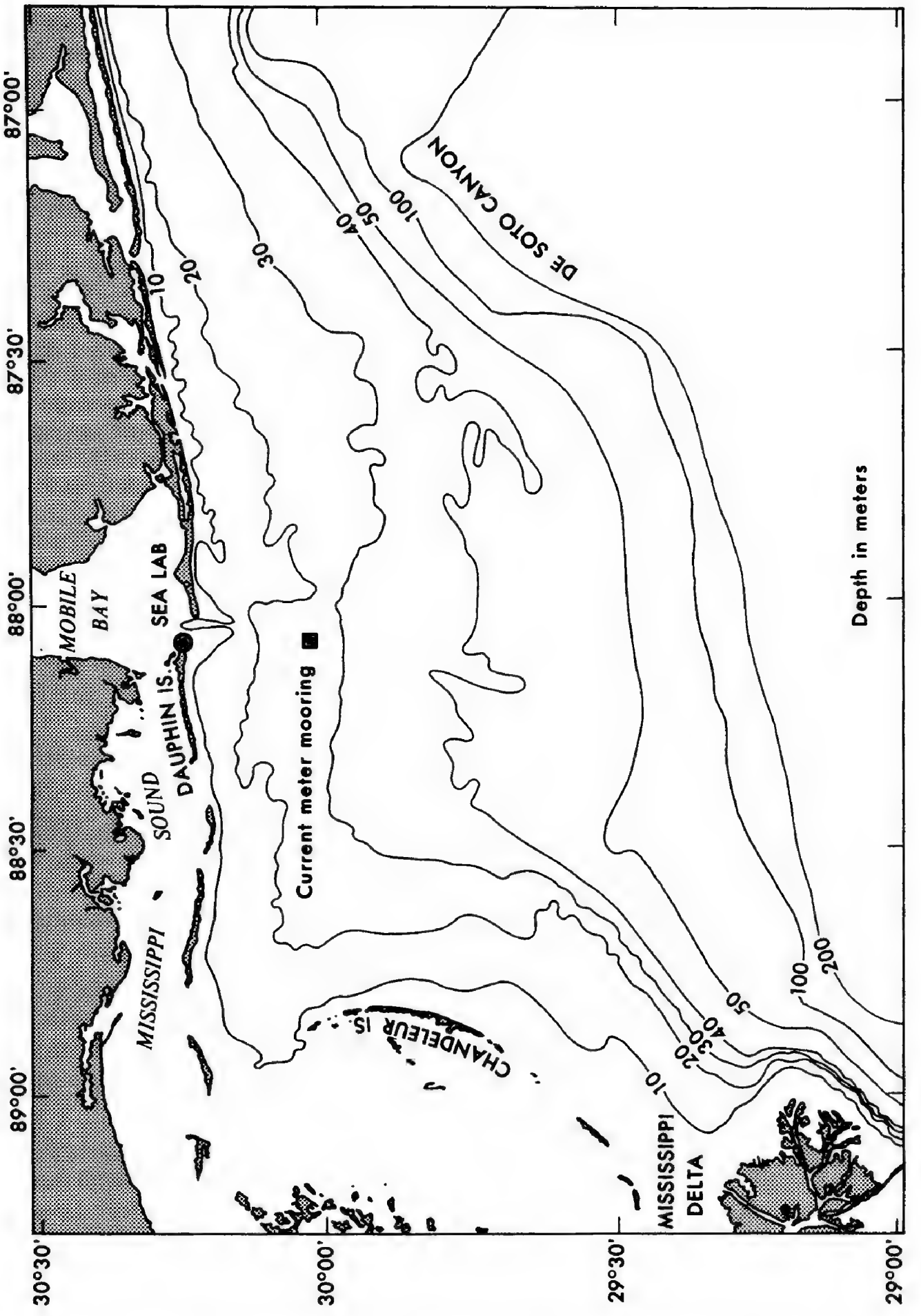


FIG. 1. Map of the northern Gulf of Mexico east of the Mississippi River delta.

Wind data were obtained at 3-hour intervals from the Dauphin Island Sea Lab meteorological station. The cross-shelf and alongshore wind stress components were computed using a quadratic law with a constant drag coefficient of $1.2 \times 10^{-3}$. Hourly sea level data were also obtained from the NOAA/NOS tide gauge at Dauphin Island. They were adjusted for the barometric effect (1 mb ~ 1 cm, with Dauphin Island Sea Lab atmospheric pressure data) prior to the analysis.

The current, wind stress, and adjusted sea level time series were low-pass filtered to remove the tidal, inertial, and other high-frequency oscillations. [A Lanczos cosine taper spanning 121 hours with a half-power point of 34 hours was used. Amplitude response was nil at 1 cpd (cycle per day), 50% at 0.7 cpd, and 95% at 0.5 cpd.] The low-pass series were subsampled at 3-hour intervals.

The 1976 current meter record showed abnormally high speeds. Upon examining the raw data from a complex demodulation analysis, we found that tidal current speeds were about three times larger than during the other two seasons. Since the tidal amplitudes (calculated from the sea level data) in the 3 years were almost identical, and we had no reason to suspect an anomalously large baroclinic tide, we concluded that a scaling error was the cause of the high speeds. This error may have been introduced in setting the speed range of the current meter (the meter was lost in a subsequent winter experiment and cannot be checked to verify our speculation). In presenting the results, we thus artificially reduce the speed of 1976 currents to one-third their original values. This scaling, however, has no effect on calculation of the mean flow direction, nor on the cross-spectrum analysis.

## RESULTS

The low-passed time series of wind stress, current, and sea level for the three summer seasons are plotted in Fig. 2. The wind was generally mild with occasional bursts spaced about 10 days apart or longer. The magnitude of the wind stress during these events, however, seldom exceeded 1 dyne $cm^{-2}$. The current was also weak; the strongest currents were only about 5 cm $s^{-1}$ in the cross-shelf direction, and 15 cm $s^{-1}$ in the alongshore direction. Sea level had less high-frequency variability than the wind and current records. The range of variation was about 30–40 cm in each of the study years.

Table 1 shows basic statistics of the wind stress, current, and sea level in each record. The orientation of the mean wind stress varied from year to year, but the magnitude was always larger in the alongshore direction. The mean alongshore wind was toward the east in 1976, and westward in 1978 and 1979. This shift was also reflected in the mean alongshore current. It is also noted that the magnitude of the alongshore current was almost proportional to the alongshore wind stress, a 0.1 dyne $cm^{-2}$ wind stress driving a 3.0 to 3.5 cm $s^{-1}$ current. These results suggest that the steady-state alongshore momentum balance is between wind stress and bottom friction, and the latter can be described by the linear friction law [*i.e.*, $\tau_{by} = \rho C_D \langle V \rangle_{rms} V$; Csanady (1976)]. With a calculated rms velocity of 5 cm $s^{-1}$, the relationship between wind and current implies a bottom drag coefficient $C_D = 6 \times 10^{-3}$, which is consistent with values found on other broad continental shelves (*e.g.*, Scott and Csanady 1976). More importantly, since the same result is reached whether the wind was toward the east or the west, such frictional balance excludes any other mechanisms (*e.g.*, an alongshore pressure gradient, or the Loop Current) as driving the mean flow.

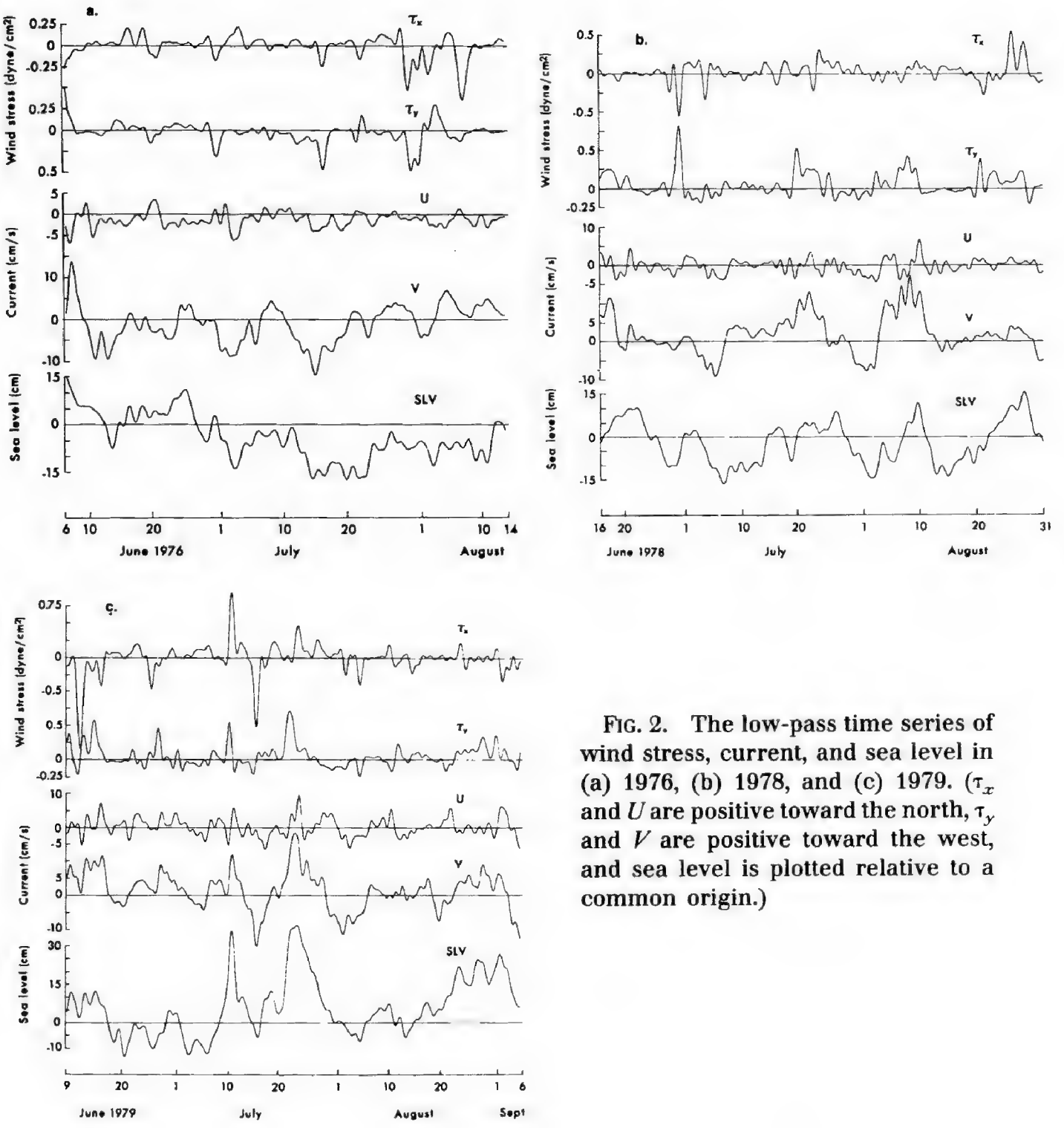


FIG. 2. The low-pass time series of wind stress, current, and sea level in (a) 1976, (b) 1978, and (c) 1979. ($\tau_x$ and $U$ are positive toward the north, $\tau_y$ and $V$ are positive toward the west, and sea level is plotted relative to a common origin.)

TABLE 1

**Mean, standard deviation, and vector mean of the wind stress, current, and sea level data.**

| | | Wind Stress (0.1 dyne cm$^{-2}$) | | | | Current (cm s$^{-1}$) | | | | Sea Level | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Duration Days | $\tan x$ (Northward) | | $\tan y$ (Westward) | | $U$ Vector* | $V$ (Northward) | | (Westward) | Vector* | cm |
| 1976 | 70 | -0.09 | 1.33 | -0.30 1.18 | 0.31 | (106°) | -1.32 1.72 | -1.08 | 4.54 1.71 | (141°) | -4.25 7.20 |
| 1978 | 78 | 0.22 | 1.21 | 0.54 1.49 | 0.58 | (-68°) | -0.23 1.82 | 1.90 | 4.95 1.91 | (-97°) | -1.80 7.50 |
| 1979 | 89 | -0.11 | 2.24 | 0.47 1.57 | 0.48 | (-103°) | 0.19 2.63 | 1.43 | 5.54 1.44 | (-83°) | 6.22 11.33 |

*The vector mean is expressed in the form of magnitude (direction), where the angle of direction is measured clockwise from the north.

The mean cross-shelf current was about an order of magnitude smaller than the mean alongshore current in 1978 and 1979. However, in 1976, the cross-shelf current was exceptionally strong and directed offshore, which made the resultant flow deviate considerably from the local coastline orientation. The cause of the large cross-shelf component is not clear. 1976, though, was also anomalous because of a mean easterly directed summer wind and apparent strong northward intrusion of the Loop Current (Vukovich *et al.* 1979). As the isobath trends east of the mooring are not parallel to the coastline, the topography may also play a role in turning the easterly flow off the shelf.

The time series plots (Fig. 2) visually show that the large events in the alongshore wind stress, alongshore current, and sea level records are coherent and in phase; a westward current was associated with a westward wind and a rise of sea level at the coast. The relations between these three variables can further be quantitatively investigated with cross-spectrum analysis (a 10-day lag window was used; the corresponding frequency resolution is 0.05 cpd, and the degrees of freedom are 18, 20, and 23 for the 1976, 1978, and 1979 data, respectively).

The spectra of alongshore current indicate a distinctive energy peak at a frequency of 0.05 cpd for all three summer seasons, and the energy drops rapidly toward high frequencies (Fig. 3). In other words, most of the

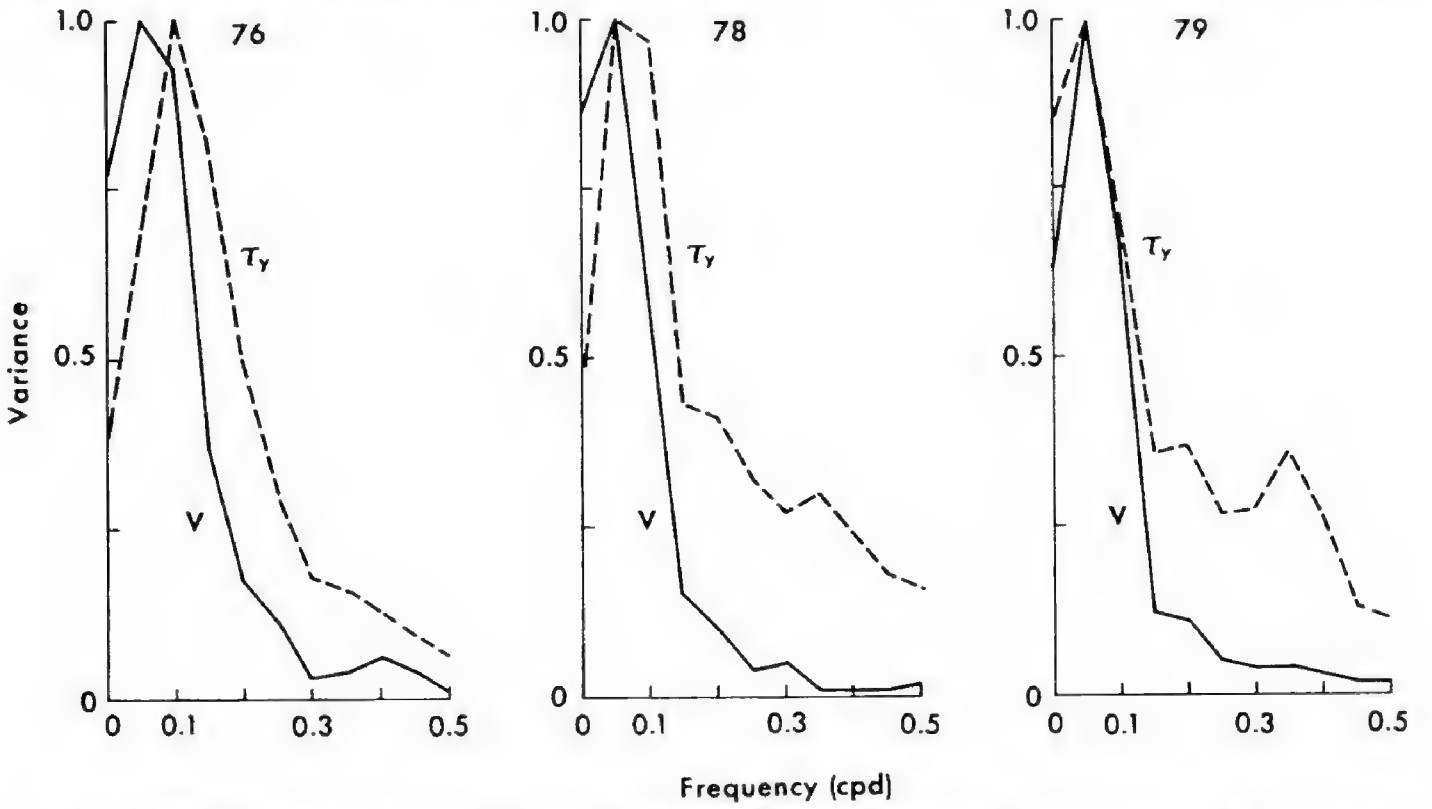


FIG. 3. The normalized power spectra of alongshore current ($V$) and alongshore wind stress ($\tau_y$) in the three study seasons.

fluctuations in alongshore current occurred at time scales of about 20 days. Similar low-frequency energy peaks are also found in the alongshore wind stress spectra (Fig. 3). However, a significant part of the wind energy is also contained in the high-frequency band. This is particularly true for the data

of 1979, where two additional energy peaks appear at time scales of 5 and 3 days.

The correlation between the alongshore current and wind stress is indeed significant at low frequencies (Fig. 4). The coherence squared is above the

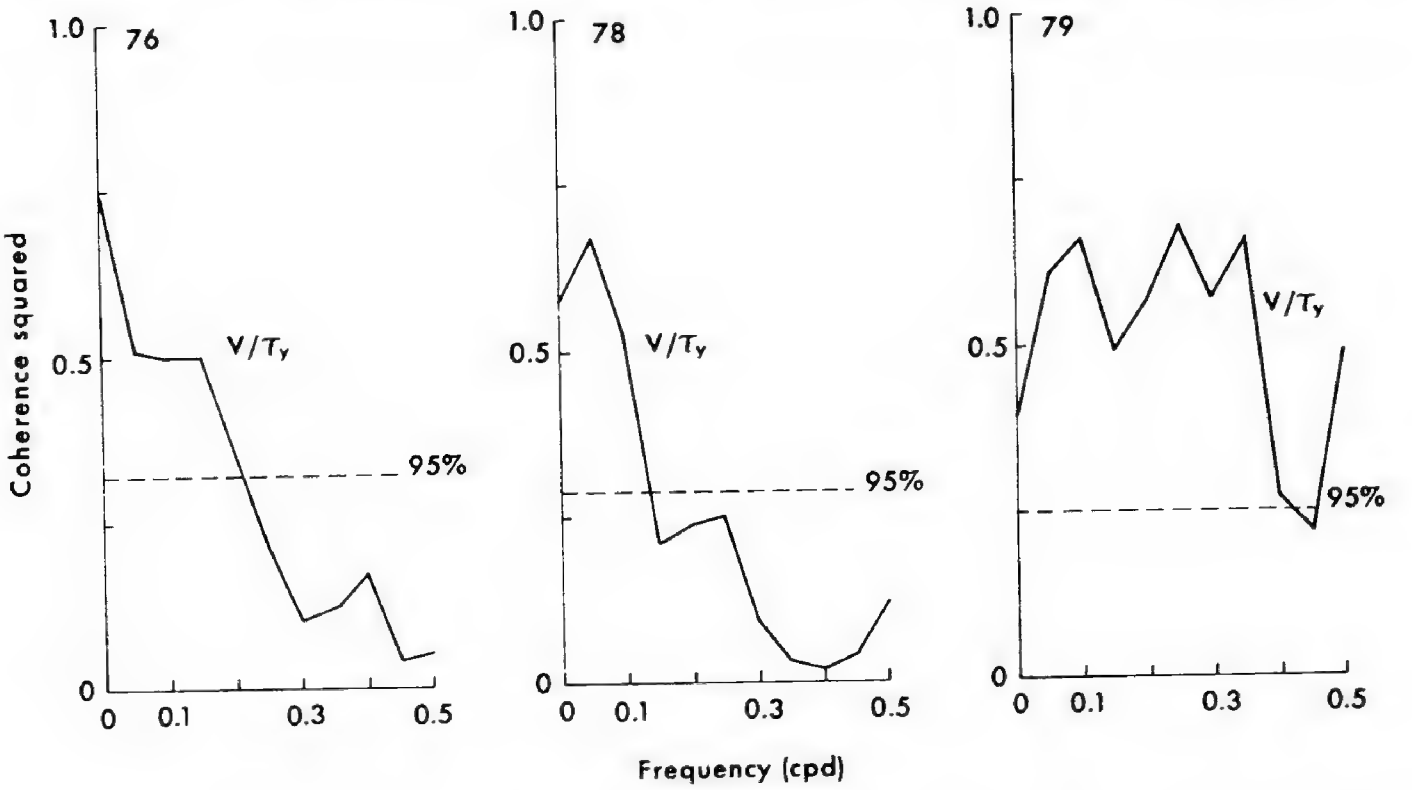


FIG. 4. The coherence squared between the alongshore current ($V$) and alongshore wind stress ($\tau_y$) in the three study seasons.

95% significance level at time scales longer than 7 days for all three summers. At shorter periods the coherence drops, except in 1979, when the high coherence extends up to the time scale of 3 days. These results suggest that the alongshore current is most responsive to long-period wind variations of a week or longer.

The sea level spectra are red (figures not shown), i.e., most of the energy is contained in the very low frequency band. The coherence between sea level and alongshore wind varies from record to record (Fig. 5): the 1976 data are coherent only at zero frequency, the 1978 data at time scales longer than 4 days, and the 1979 data at all time scales of interest. Since the alongshore wind in 1976 differed from the other 2 years in that its fluctuations were mostly due to the change of strength in the eastward component (Fig. 2), the relatively low coherence between sea level and alongshore wind stress implies that the easterly wind was not as efficient as the westerly wind in inducing coastal sea level changes.

The coherence between sea level and alongshore current is significant at time scales between 10 and 20 days for all three records. At other time scales the correlation is very selective, *i.e.,* high coherence appears at different frequencies in different years, and it does not necessarily coincide with the frequencies of the significant fluctuations in the alongshore current. These

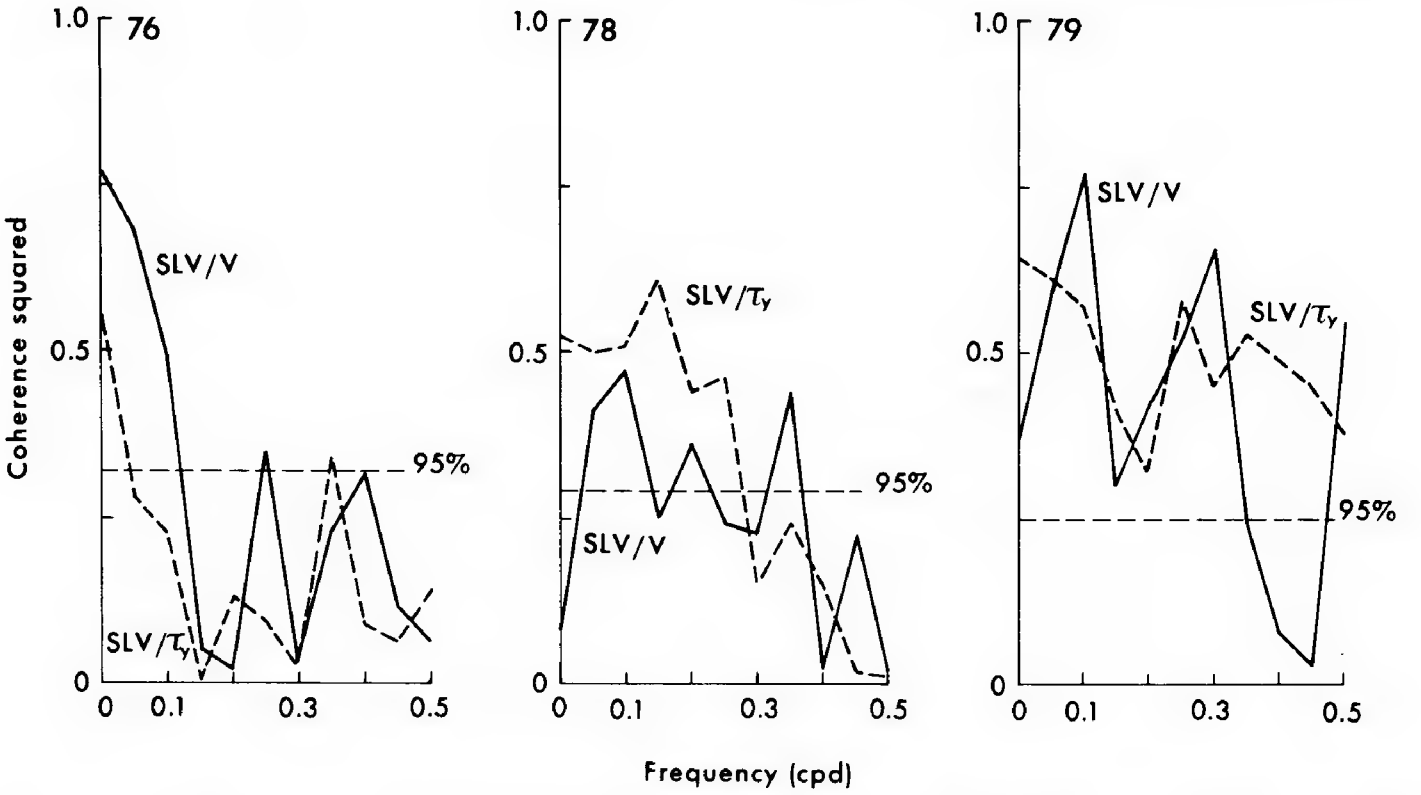


FIG. 5. The coherence squared between the sea level ($SLV$) and alongshore current ($V$) and alongshore wind stress ($\tau_y$) in the three study seasons.

results suggest that a geostrophic balance between the cross-shelf pressure gradient and alongshore current only exists for the long-period motions. At shorter periods, coastal sea level seems to be affected by other factors. Hence, sea level data cannot serve as a good linear predictor of the shelf water response to local wind forcing along this part of the coast.

## DISCUSSION

Current measurements from three different summers indicate that the mean alongshore motion off the Alabama coast is predominantly wind-driven. As the wind varies from year to year, a permanent summer circulation pattern cannot be determined; a net flow in either longshore direction is possible. Cross-shelf motion is generally negligible when the alongshore flow is toward the west, but there is a persistent offshore motion associated with the eastward flow observed during the summer of 1976. It is interesting to note that aperiodic reversals of the flow along the shelf break in this region have been inferred from drift bottle returns (Ichiye *et al.* 1973).

Analysis of subtidal fluctuations of alongshore current and sea level has shown that they are correlated with the alongshore wind stress at time scales longer than a week. Also, the shelf water response is strongest at about 20-day time scales, although the wind energy is not restricted to this particular frequency band. At time scales shorter than a week, the coherence between these three variables differs substantially from one year to another, and it is generally below the 95% significance level.

Since current measurements were made only at a single point, the cause of the frequency-dependent response cannot be completely determined. A

plausible explanation lies in the effect of the local density structure, as the current meter was moored in the lower layer of a strongly stratified regime. At low frequencies, a frictional balance is expected, and the three variables are observed to be highly coherent. At higher frequencies, momentum from the wind is not readily transferred across the pycnocline to affect the lower layer. Ekman flux within the upper layer, though, still causes a rise or fall of coastal sea level (Chuang *et al.* 1979), which explains why sea level is more coherent with wind stress than is the current.

In addition to the effect of density stratification, the alongshore variations of coastal geometry may also play a role, particularly near the Chandeleur Islands, where the coastline orientation changes by nearly 90°. Bennett and Magnell (1979), in an attempt to model the circulation in the New York Bight, found that the transient behavior of current is strongly influenced by the effect of wind setup at Long Island, whereas the low-frequency motion can be described satisfactorily by a local Ekman model. Thus, a more complete coverage of current measurement in both vertical and alongshore directions is essential to understanding the circulation on the continental shelf east of the Mississippi River delta.

## ACKNOWLEDGMENTS

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## LITERATURE CITED

BENNETT, J. R. and B. A. MAGNELL. 1979. A dynamical analysis of currents near the New Jersey coast. *Journal of Geophysical Research.* 84:1165–1175.

CHUANG, W.-S., D.-P. WANG and W. C. BOICOURT. 1979. Low-frequency current variability on the southern Mid-Atlantic Bight. *Journal of Physical Oceanography.* 9:1144–1154.

CSANADY, G. T. 1976. Mean circulation in shallow seas. *Journal of Geophysical Research.* 81:5389–5400.

DRENNAN, K. L. 1968. Hydrographic studies in the northeast Gulf of Mexico. Technical Report 68-0-1. Environmental Sciences and Engineering Laboratories, Gulf South Research Institute, New Iberia, Louisiana, 111 pp.

HURLBERT, H. E. and J. D. THOMPSON. 1980. A numerical study of Loop Current intrusions and eddy shedding. *Journal of Physical Oceanography.* 10:1611–1651.

ICHIYE, T., H.-H. KUO and M. R. CARNES. 1973. Assessment of currents and hydrography of the Eastern Gulf of Mexico. Texas A and M University, Dept. of Oceanography, Contribution No. 601.

LEIPPER, D. 1954. Physical oceanography of the Gulf of Mexico: Gulf of Mexico, its origin, waters, and marine life. *Fishery Bulletin Fish and Wildlife Service, U.S.* 55(89):119–137.

MURRAY, S. P. 1972. Observations on wind, tidal, and density-driven currents in the vicinity of the Mississippi River delta. In D. J. P. Swift, D. B. Duane, and O. H. Pilkey (eds.) *Shelf Sediment Transport,* pp. 127–142, Dowden, Hutchinson and Ross, Stroudsburg, PA.

SCOTT, J. T. and G. T. CSANADY. 1976. Nearshore currents off Long Island. *Journal of Geophysical Research.* 81:5401–5409.

SCHROEDER, W. W. and CROZIER, G. F. 1974. Hydrographic and current structure on the waters of the continental shelf of the northeastern Gulf of Mexico. In R. E. Smith (ed.)

*Marine Environmental Implications of Offshore Drilling in the Eastern Gulf of Mexico,* pp. 395–404. State University System of Florida, Institute of Oceanography, 74-4, St. Petersburg, Florida.

SMITH, N. P. 1978. Low-frequency reversals of nearshore currents in the northwestern Gulf of Mexico. *Contributions in Marine Science.* 21:103–116.

_____. 1979. An investigation of vertical structure in shelf circulation. *Journal of Physical Oceanography.* 9:578–584.

_____. 1980. Temporal and spatial variability in longshore motion along the Texas Gulf Coast. *Journal of Geophysical Research.* 85:1531–1536.

THOMPSON, P. A., JR. and T. D. LEMING. 1978. Seasonal description of winds and surface and bottom salinities and temperature in the northern Gulf of Mexico, October 1972 to January 1976. *NOAA Technical Report or NMFS SSRF-719.* U.S. Dept. of Commerce.

VUKOVITCH, F. M., B. W. CRISSMAN, M. BUSHNELL and W. J. KING. 1979. Some aspects of the oceanography of the Gulf of Mexico via satellite and in situ data. *Journal of Geophysical Research.* 84:7749–7768.

*Contributions in Marine Science.* (1982) Vol. 25:133–148.

# SEDIMENT TRANSPORT ON THE CENTRAL LOUISIANA CONTINENTAL SHELF: IMPLICATIONS FOR THE DEVELOPING ATCHAFALAYA RIVER DELTA

Charles E. Adams, Jr., John T. Wells and James M. Coleman

*Coastal Studies Institute, Louisiana State University, Baton Rouge, Louisiana 70803*

## ABSTRACT

Near-bottom current velocity measurements made at a continental shelf site off the central Louisiana coast over a 4½-month period form the basis for an analysis of sediment transport in the benthic boundary layer. The winter flow field is represented by a tidally dominated regime superimposed on a slow wind-driven westward drift. Mean westerly flow frequently is interrupted by brief periods of intense eastward flow resulting from the passage of continental cyclonic storms. Cross-shelf flow is conspicuous throughout the data record. Bottom shear stress as calculated from the quadratic relationship was high enough on eight separate occasions to resuspend the coarsest material (very fine sand, 3.5ϕ) found at the study site. The presence of quantities of suspended sand in the water column during the periods of high bottom stress was indicated also by an analysis of the logarithmic layer near the bottom. Predominance of eastward displacements during the periods when bottom stress is high enough to cause resuspension of the sand-sized sediments, together with small quantities of silts and clays, suggests that sand-sized material is moved selectively eastward and offshore, while the finer sediments are moved downcurrent with the mean flow. As Atchafalaya Bay continues to fill and Atchafalaya River sediment is carried out onto the continental shelf, much of the coarser material should remain in the immediate vicinity of the delta front, and perhaps move to the southeast and thus tend to skew the coarser size components of the advancing delta in that direction.

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## INTRODUCTION

The Atchafalaya River, in south-central Louisiana (Fig. 1), as a distributary of the Mississippi River, has carried large volumes of water and sediment for over 400 years (Fisk 1952). During much of this time the sediment load carried by the river was deposited within the many lakes and other natural catchment basins in the upper reaches of the river. In the decade beginning in 1950, fine, clay-sized sediments began appearing in Atchafalaya Bay as a result of the filling of the catchment basins upriver. In the following decade (1962–1972) the river sediment load coarsened (Roberts *et al.* 1980). The dominance of silt- and sand-sized material carried by the river during this period resulted in the development of distal and subaqueous bars (van

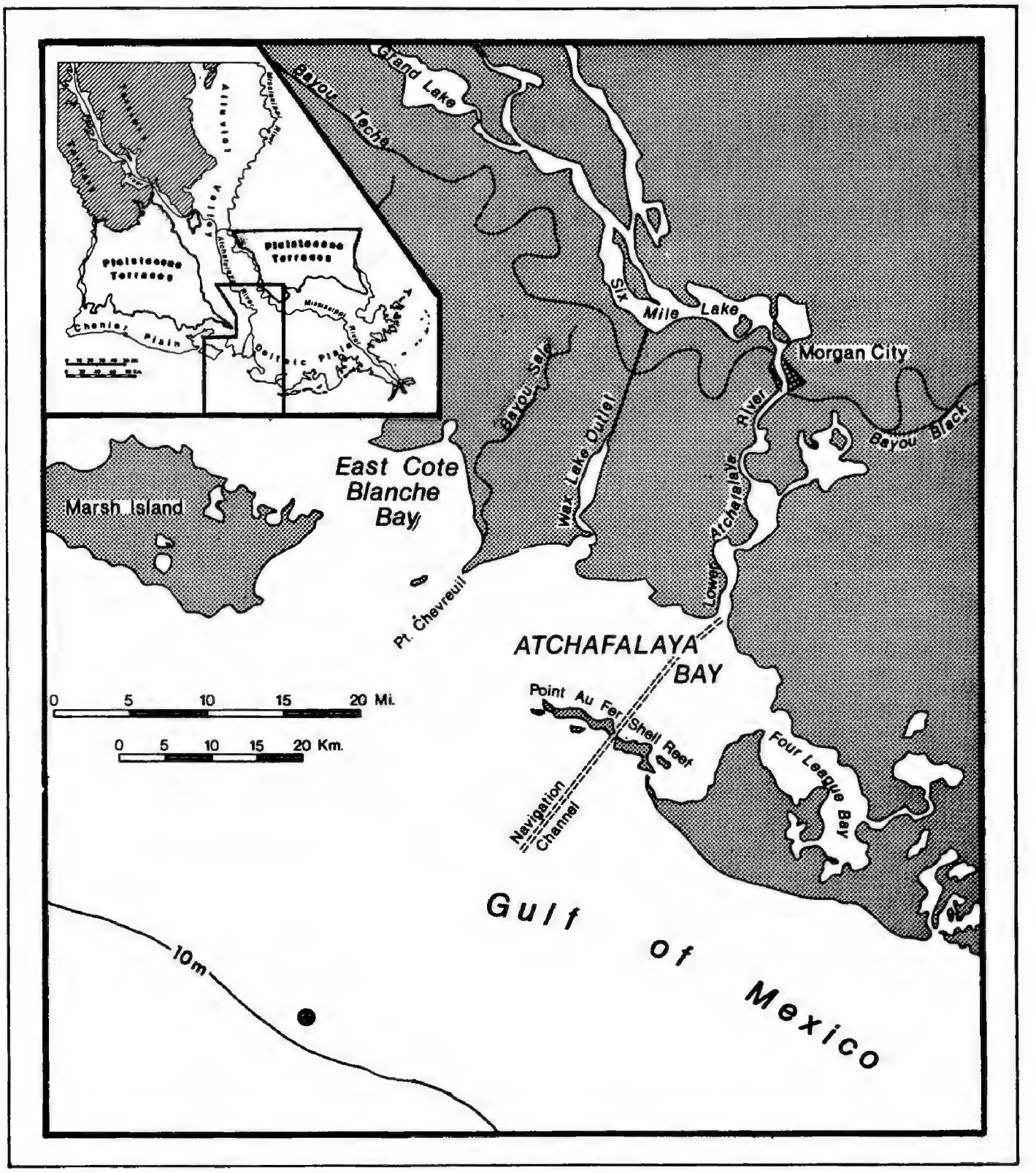


FIG. 1. Location map of the lower Atchafalaya River and Bay and the continental shelf current monitoring site (solid circle) (modified from Roberts *et al.*, 1980).

Heerden and Roberts 1980) associated with the now rapidly prograding delta in Atchafalaya Bay. For about the last 10 years the delta has been growing subaerially. As the bay continues to fill with sediment, more coarse material will be available for delivery to the exposed coast and beyond to the continental shelf. A continued sediment supply should eventually lead to the emergence on the continental shelf of a river delta not dissimilar from that of the modern Mississippi River delta. The presence of such a feature clearly can have a profound influence on local shelf circulation patterns and coastal morphology, as has been suggested by Murray (1976) in the case of the

modern Balize Delta. Changes in currents and coastal features are certain to have an effect on practical matters such as coastal wetlands management and production of the fisheries.

The purpose of this paper is to report on the implications of some near-bottom current measurements made on the continental shelf offshore of the developing Atchafalaya River delta. The objective of the data analysis was to gain a better understanding of the near-bottom flow in the region and to determine relationships between the flow and the sediment transport fields. Thus it should be possible to make inferences concerning processes and patterns of future delta growth. The data encompasses a 4½-month period during the winter when wind-driven shelf currents which are responsible for the sediment transport process are most energetic.

## ENVIRONMENTAL SETTING

### Sedimentary Geology

Holocene sediments of the Atchafalaya Basin are underlain by the Pleistocene Prairie Formation, a young Pleistocene fill that consists of stiff, oxidized, clay-sized sediments. Following the Holocene rise in sea level, the Mississippi River built five major delta complexes consisting of at least 16 separate lobes (Frazier 1967). Three of these delta complexes, the Maringouin, Teche, and Lafourche, covered Atchafalaya Bay and areas offshore with alluvial-deltaic sediments that now form the base for Atchafalaya River sedimentation.

The quantity and size distribution of sediments available to Atchafalaya Delta are related to the modern history of Atchafalaya River and basin. Although the Atchafalaya River was a distributary of the modern Mississippi River in the mid-1500s, it became a major source of sediments transported to the coast only after log jams were cleared in the 1800s (Fisk 1952). A natural channel had become well established by the mid-1900s and volume of flow down the Atchafalaya River continuously increased. The suspended sediments that bypassed the upstream catchment basins eventually were deposited in Atchafalaya Bay and on the inner continental shelf as prodelta clays. Following the flood of 1973, sand-sized distributary-mouth bar sediments emerged subaerially in the bay as a new delta. Silts and clays continued to be carried to the distal parts of the bay and behind the Point Au Fer shell reefs.

The paucity of data seaward of Atchafalaya Bay precludes a firm understanding of the most recent sedimentation patterns. However, unpublished data from shallow cores, bottom probes, and side-scan sonographs suggest that clays and silts dominate the inner shelf environment to a water depth of 10–20 m. Isolated shoals, perhaps the remnants of former delta lobes, may be largely sand-sized material. As the Atchafalaya Delta progrades seaward, introduction of fine sands to the shelf as suspended-load transport during floods will become more common.

### Coastal Circulation

The net motion of the waters along the central Louisiana coast west of the Mississippi Delta is to the west (Murray 1976) due to the predominance of winds from an easterly direction throughout the year. During winter, however, migrating continental low-pressure centers frequently intrude into the northern Gulf of Mexico, bringing northerly winds which are the strongest of the entire year (Brower *et al.* 1972). These northerly winds are associated with frontal passages. Depending on the angle between the front and the Louisiana coast, the wind may have either a westerly or an easterly directed longshore component. In the former case, the local wind augments the net westward flow; in the latter, the wind frequently is of sufficient

magnitude to generate a vigorous easterly directed flow at all levels in the water column. The data to be presented indicate that westerly directed currents associated with a frontal passage are relatively unimportant. The passage of 15 to 20 frontal systems through the Louisiana coastal region during a normal winter is common (Brower *et al.* 1972).

Although there are definite and strong relationships between the current system along the Louisiana coast and the patterns of regional and local wind systems, other driving factors are also important. For example, during summer, when winds are generally weak, tidal forces become dominant (Murray 1976) and transshelf motions associated with the rotary diurnal tide may mask the slow westward drift. During spring floods, the buoyant plume of the Mississippi and Atchafalaya rivers may create pressure gradients that strongly reinforce the net westward motion.

## OBSERVATIONAL DATA

The oceanographic data presented here are from two bottom-mounted platforms located within 15 m of each other and approximately 50 km offshore at a continental shelf site off the central Louisiana coast (Figure 1). An array of these platforms was deployed over a 1-year period by the National Oceanic and Atmospheric Administration in an effort to characterize the physical oceanography of Louisiana shelf waters. Detailed descriptions of the instrumentation, calibration procedures, and platform configurations are given by Frey and Appell (1981); those aspects that may be expected to have an influence on the interpretations to be made here are summarized below.

The bottom at the mooring site is relatively flat with a regional slope of about 0.0006 (0.03°). Local isobaths which parallel the shoreline here trend about 70° west of true north. Bottom sediments as described by Hausknecht (1980) consist primarily of sand-sized material (>70%) with lesser amounts of silt- and clay-sized particles present. The sand-silt ratio was seasonably variable; the ratio ranged from an autumnal low of about 3.5 to a vernal high of about 5. The sand fraction was always at least moderately well sorted, with an average predominant mode of 3.5 $\phi$. An important point is that the sediments are essentially noncohesive (see, *e.g.*, Owen 1977). For sufficiently small concentrations, a sediment-water mixture therefore should behave as a Newtonian fluid.

The two rigid platforms, set on the bottom in 9 m of water, each supported two Grundy current meters with rotors that turn in either direction. The meters were located at heights of 1.0 m and 3.0 m above the footpads on one platform and at heights of 2.0 m and 4.0 m above the footpads on the other. The meter at 4.0 m failed to provide validated data (H. Frey, personal communication). There is a degree of uncertainty associated with both the height of the current meters above the bottom and the relative separations between the meters at 1.0 m and 3.0 m and the meter at 2.0 m which results from current scour about the base of the platform. As an example of the magnitude of the uncertainty, on March 12, 1979, the footpads were observed to be approximately 0.5 m below the sediment-water interface (H. Frey, personal communication). For definiteness, the current meters are hereafter referred to as the 1-m, 2-m, and 3-m current meters, the values representing approximate heights above the bottom. One of the platforms supported a pressure-type wave gauge also.

Current as measured by the current meters is the average value over the sampling interval, which was set at 10 min. Because the averaging interval is much longer than the period of ordinary surface gravity waves, and because the meters respond to backflow as well as forward flow (although not necessarily with equal efficiency), the contribution of wave orbital motions to the observed mean current speed is thought to be small. Continuous current meter records at the three levels were available for the 4½-month period of interest except for the 5-day period (January 23–28, 1979) during which no current meter data are available. For analytical purposes, current velocity was resolved into long-isobath ($u$, positive to the east) and cross-isobath ($v$, positive onshore) components. Significant wave heights based on spectral estimates were available only for the period November 1, 1978, to January 22, 1979.

## DATA ANALYSIS AND RESULTS

### Near-Bottom Flow

The general character of the flow field during the 4½-month period as represented by the current meter at the 1-m level is shown in a progressive vector plot of water motion (Fig. 2) in which the $x$-axis is long-isobath and

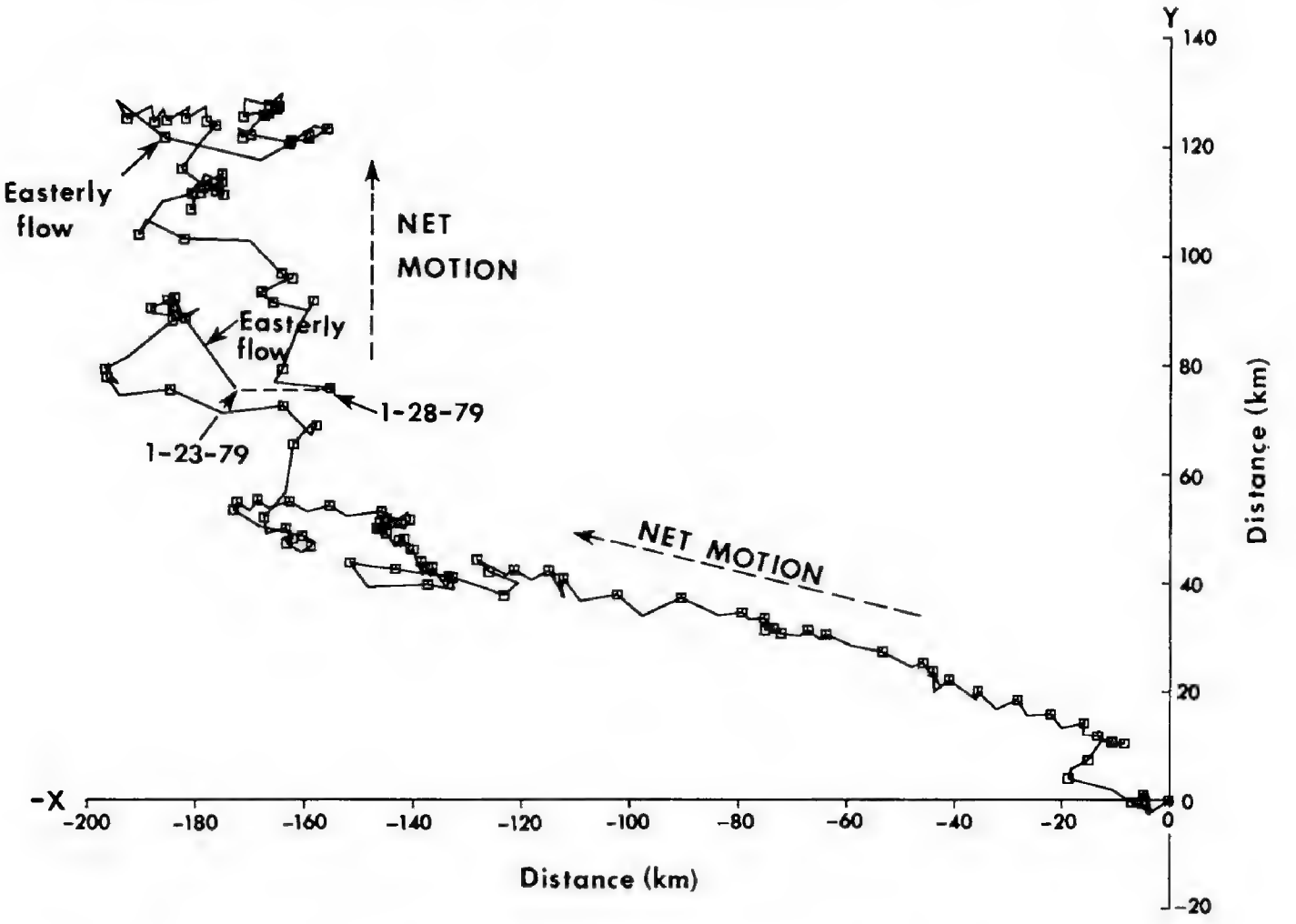


FIG. 2. Progressive vector plot of water displacement at the 1-m level for the period November 1, 1978, to March 12, 1979. Open squares are drawn after each 24-hour interval. The data have been smoothed over 12 hours. Note the two periods of prolonged eastward movement, marked by arrows.

the $y$-axis is onshore. The data for Figure 2 have been smoothed over 12 hr, thus concealing the rotary nature of the flow, which Daddio *et al.* (1978) have attributed to wind-forced inertial currents. The net flow during the study period was in a westerly direction with a substantial onshore component. From early February to the end of the data record, net motion was dominantly cross-isobath and onshore. Although caution must be used in making a Lagrangian interpretation of Eulerian data, particularly in proximity to a boundary (see, for example, Smith, N. P. 1977), it is clear that in this area transshelf motions during the winter may be as important to the dispersion of particulate materials as are long-shelf flows. The net speed of the water during the entire 4½-month observation period was less than 5 cm $s^{-1}$ to the west.

In contrast to the net westerly drift were two conspicuous periods of about 1 day each in which the water moved rapidly in an easterly and off-shelf direction (Fig. 2). Both of these easterly flow events coincided with frontal passages, which were characterized by high winds from a northerly direction and by relatively high surface waves. Current speed at the 1-m level during these two easterly flow events exceeded 50 cm $s^{-1}$.

The $u$ and $v$ components of velocity at the 1-m level are shown in Figure 3A and 3B, respectively. The $v$ component clearly exhibits the diurnal tidal signal almost continuously throughout the record length. Subtidal events are more evident in the $u$ component than in the $v$ component record, which suggests that subtidal motions (wind-forced events) are principally directed parallel to the isobaths. The two easterly flow events mentioned above are clearly evident in the velocity component records, with peak velocities occurring at $t \cong 1945$, 2795 hr.

## Boundary Shear Stress

Bottom shear stress is a fundamental quantity in sediment transport problems and knowledge of its magnitude is crucial in determining the mode of transport, *i.e.,* bed or suspended load. One method of estimating shear stress is with the quadratic relationship, which may be written as

$$\tau_o = \rho C_D U_{100}^2 \tag{1}$$

where $\rho$ is fluid density, $C_D$ is the drag coefficient, and $U_{100}$ is the mean current speed 100 cm above the bottom ($U_{100} = (u_{100}^2 + v_{100}^2)^{1/2}$). In the calculations here, $C_D$ = constant = $1.4 \times 10^{-3}$.

The critical suspension curve of Bagnold (1966) as revised by McCave (1971) indicates that sediment finer than about 2$\phi$ will be transported almost entirely in suspension. The critical suspension curve also yields a critical bottom stress for resuspension of the 3.5$\phi$ sediments as $\tau_{cr} = 1.7$ dynes $cm^{-2}$. As may be seen from the time series plot of shear stress (calculated from Equation (1)) in Figure 3C, the shear stress required to resuspend the 3.5$\phi$ sand is exceeded briefly on five separate occasions between November 1, 1978, and January 21, 1979. During four of these periods of elevated bottom stress, the flow near the bottom is directed toward the east ($+u$) (Fig. 3A). A prolonged period of super-critical bottom stress, during which resuspension of significant quantities of sand-sized sediments might be expected, does not occur until January 20, 1979, when $\tau_o$ reaches a maximum of about 7 dynes $cm^{-2}$ and $\tau_o > \tau_{cr}$ for approximately 15 hours. From January 29 to March 12, 1979, $\tau_{o_{max}} \cong 4.5$ dynes $cm^{-2}$. The dynamics of the latter event was investigated by Adams in an earlier study. In all cases of high bottom stress the flow event resulted from the passage of a frontal system.

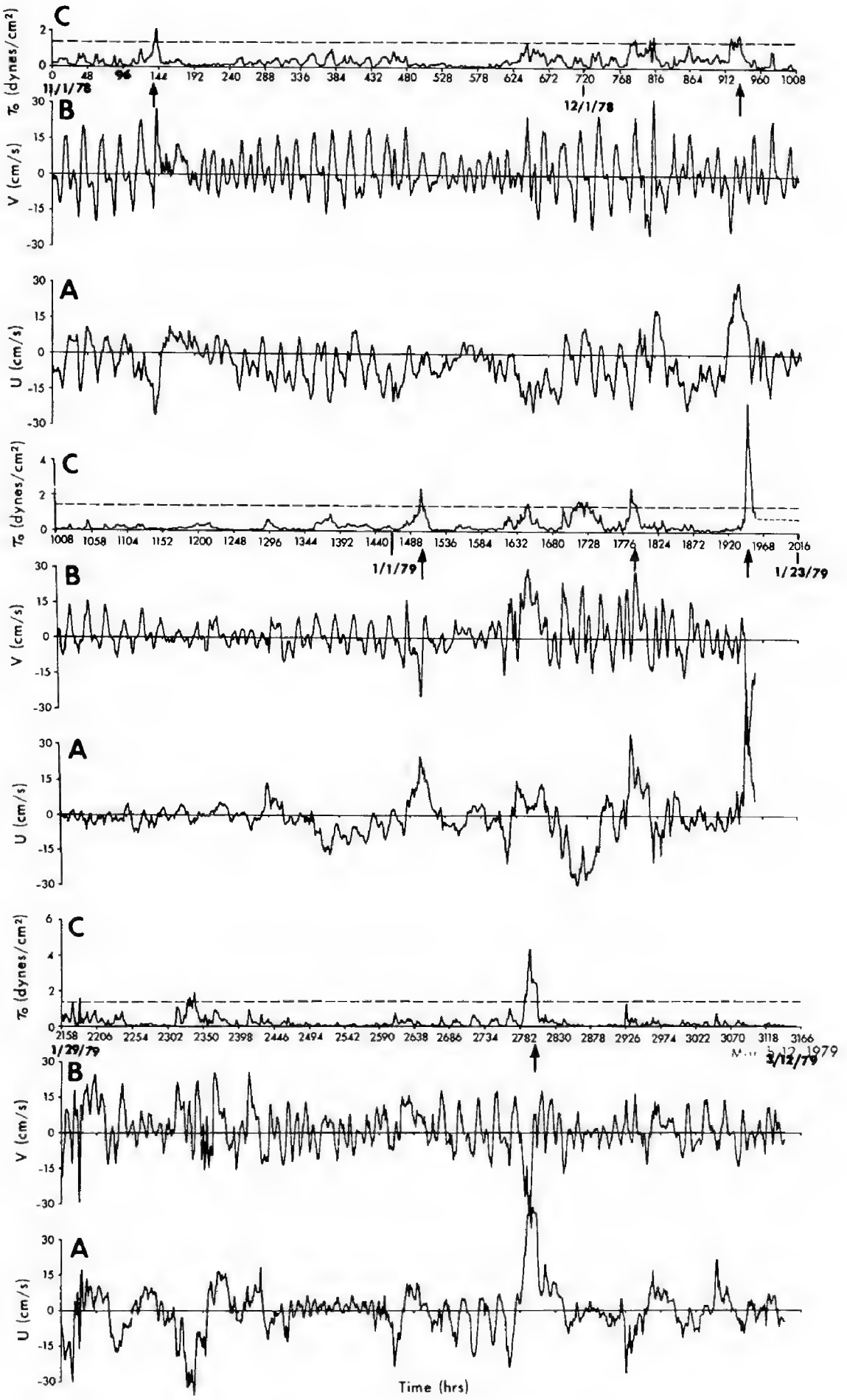


FIG. 3. Plots of $u$ (A) and $v$ (B) components of velocity at the 1-m level and time series of bottom stress ($\tau_o$) ($C$) as calculated from Equation (1) for the period November 1, 1978, to March 12, 1979. The straight line represents the critical shear stress for a 3.5$\phi$ size component ($\tau_{cr} \cong 1.7$ dynes cm$^{-2}$). Logarithmic layer analysis was made for the data between 2712 hr $< t \leqq$ 2832 hr.

## Boundary Layer Characteristics of the Flow Field

In a steady, neutrally stable boundary shear flow, a logarithmic layer is present immediately above the boundary. The velocity in this logarithmic layer is given by

$$U = \frac{u_*}{\kappa} \ln \frac{z}{z_o} \tag{2}$$

where $U$ is mean current speed, $u_* \equiv (\tau_o/\rho)^{1/2}$ is the friction velocity associated with the mean flow, $\kappa$ is von Karman's constant ($\kappa \cong 0.4$), $z$ is the vertical coordinate, positive in the upward direction, and $z_o$ is the roughness length ($z > z_o$). The term $\kappa/u_*$ in (2) is the slope of the velocity profile when depth versus speed is plotted in log-linear coordinates. Thus, when velocity profile data are available, Equation (2) may be invoked to obtain estimates of $u_*$ (and thus $\tau_o$).

A turbulent fluid shear flow laden with sediment exhibits characteristics that distinguish it from a similar flow of a clear fluid. For a given boundary shear stress, one of the most striking differences between the two is the higher velocities at all levels in the turbid flow. This two-phase effect has been observed in the laboratory (Vanoni and Nomicos 1959) and in the marine environment (McCave 1973, Nihoul 1977). Increased velocity shear resulting from a suspension of sediment has been documented also in mathematical model studies of benthic boundary layer flows (Smith and McLean 1977; Adams and Weatherly 1981a, b). Other two-phase effects resulting from a suspension of sediment in a boundary layer flow are known also (see, *e.g.*, Adams and Weatherly 1981a, b).

In the absence of simultaneous current velocity and suspended sediment concentration profiles, it is possible to exploit the velocity shear variation in the flows of sediment-laden and clear fluids to gain additional insight into the nature and the intensity of two-phase effects and in particular to make inferences concerning the stability of sediment-laden flows. This type of approach was used by McCave (1973) in a study of suspension transport of sands by tidal currents. The same methods of analysis can be applied to the suspension transport of coarse sediments by unidirectional currents. As an example, during periods of relatively low flow, when accelerative effects are small, bottom shear stresses are low and little or no sediment erosion occurs; the velocity profile is that of an essentially clear flow. As the velocity field develops in response to strong winds, turbulent shear stresses at the bottom increase and sedimentary particles stripped from the bottom are carried along with the flow. In the absence of thermal stratification and acceleration effects, any observations of increased velocity shear can be attributed directly to suspended sediment effects. Comparison of velocity profiles in these two well-defined situations allows estimates to be made of relative suspended sediment concentrations associated with the respective flows. Because the period 2712–2832 hours (Fig. 3A, B) offered two distinctly

contrasting flow regimes, a dynamical analysis was made of the current meter data, the results of which are summarized below.

Using the method of least squares, hourly averaged velocities at the three sampling levels were fit to Equation (2). A velocity profile was defined as being logarithmic when the coefficient of determination $r^2 \geqq 0.9755$ ($r$ is the correlation coefficient). This is the $t$ test criterion for a 90% confidence level in a three-point fit.

Overall, velocity profiles satisfying the logarithmic criterion occurred about 50% of the time. An examination of the profile data showed a marked difference in the frequency of occurrence of logarithmic profiles during the early period (2712 hr $< t \leqq$ 2783 hr) when periodic influences were strong and during the wind-forced unidirectional flow episode ($t \geqq$ 2784 hr). During the former, logarithmic profiles were found in only about 40% of the data while during the latter they were found in more than 65% of the data. The wind-forced flow episode can be partitioned further into three distinct events. The first is the 10-hour period when the water column is accelerating; none of the velocity profiles for this period were logarithmic. The second is the interval 2794 hr $\leqq t \leqq$ 2805 hr, during which about 85% of the profiles were logarithmic. The interval 2806 hr $\leqq t \leqq$ 2831 hr had a percentage of logarithmic profiles similar to the preceding one; however, the slopes of the profiles were significantly larger and more variable. Thus, on the basis of the occurrence of logarithmic profiles and on the slopes of those profiles, two distinct flow events were identified for analysis. These are the intervals 2712 hr $< t \leqq$ 2783 hr and 2794 $\leqq t \leqq$ 2805. The early period was assumed to represent an episode of predominantly clear flow, while the later one was thought to be a period during which substantial quantities of sediment were being transported in suspension.

The speed data for the logarithmic velocity profiles within each of the two time intervals were averaged and those values again fitted to Eq. (2) by the least-squares method. The resulting profiles are shown in Figure 4. Of interest in these profiles are the slopes from which values of $u_*$ ($\tau_o$) presumably may be calculated, and the relative differences of this parameter among the various profiles.

## Sediment-Free Velocity Profile

The composite velocity profile for 2712 hr $\leqq t \leqq$ 2783 hr (profile 1) is characterized by a modest slope which yields $u_* = 1.0$ cm s$^{-1}$. This value of $u_*$ should be representative of the shear velocity of the mean flow, assuming that wave orbital motions have been excluded from the current meter data. Thus it is the value that may be associated with the sediment transport process in the problem being considered. Wave oscillatory currents, although not contributing significantly to the mean flow, create stresses that influence resuspension rates and must be accounted for. To a first approximation, mean and wave stresses may be added vectorially to give an estimate of the total bottom stress acting to resuspend sediment. It is noted

that the wave-current interactions are highly nonlinear (Smith, J. D. 1977; see also Grant and Madsen 1979), and estimates based on a linear superposition of components will likely result in underestimating the total stress. Inclusion of nonlinear effects, however, seems unwarranted given the nature of the wave data.

For monochromatic waves of period $T = 4\ s$, the technique presented by J. D. Smith (1977) yields $u_{*_w} \cong 0.2\ \text{cm s}^{-1}$. The subscript $w$ refers to the waves. The friction velocity at the bottom in the presence of waves and mean current for the period $2712\ \text{hr} \leqq t \leqq 2783\ \text{hr}$ thus is $u_{*_{\text{Total}}} \cong 1.2\ \text{cm s}^{-1}$ ($\tau_o \cong 1.4$ dynes $\text{cm}^{-2}$), which is less than the critical friction velocity required for resuspension of the 3.5$\phi$ sediments, according to McCave (1971). Here $u_{*_T} = u_* + u_{*_w}$. At the lower limit of validity of the McCave curve (coarse silt, about 4.5$\phi$), the critical shear stress needed for resuspension is only slightly greater than the ambient value $u_{*_T}$. For silt-sized and finer materials, the combined wave-current stress should be sufficient for resuspension. The paucity of fine-grained sediments (silts and clays) at the Louisiana shelf site during the period of study and the presence of these materials during other seasons when combined bottom stress might be expected to be lower supports this interpretation. Thus, insofar as the initial 71-hr period is representative of the local mean flow, the combined tidal-inertial and oscillatory flows are incompetent to resuspend any sediments other than the finer materials present.

## Sediment-Laden Velocity Profile

In the interval $2794\ \text{hr} \leqq t \leqq 2805\ \text{hr}$ the slope of the velocity profile (Fig. 4, profile 2) is significantly smaller than that of profile 1. The marked decrease in slope (increase in shear) is strongly suggestive of a change from a clear flow to one that is sediment laden (or at least a change from a neutral to a stably stratified flow). However, implicit in Eq. (2) is the assumption of neutral stability; thus buoyancy effects, which promote increased stability and which may have an influence on the flow dynamics, have been excluded.

From a practical standpoint, the use of Equation (2) in a stratified flow may result in spurious estimates of $u_*$. For example, as estimated from profile 2, $u_* = 7.6\ \text{cm s}^{-1}$, which appears to be an abnormally high value for the observed current velocities. Another estimate of bottom stress may be obtained by assuming that the downstream flow is frictional, *i.e.,* that surface wind stress is balanced by bottom stress ($\tau_w - \tau_o = 0$). Longshore coastal currents satisfying this simple frictional balance have been observed by Huyer *et al.* (1978) and by Winant and Beardsley (1979). Data from Figure 3A, B indicate that accelerations during the period $2794\ \text{hr} \leqq t \leqq 2795\ \text{hr}$ are ($10^{-3} - 10^{-4}\ \text{s}^{-1}$). With a vertical eddy viscosity $K_v = 0\ (10^2)$, the diffusion term in the long-isobath momentum equation is one or two orders of magnitude larger than the temporal acceleration term. If the long-isobath pressure gradient may be assumed small (no larger than the acceleration term), then the frictional assumption is a reasonable first approximation for

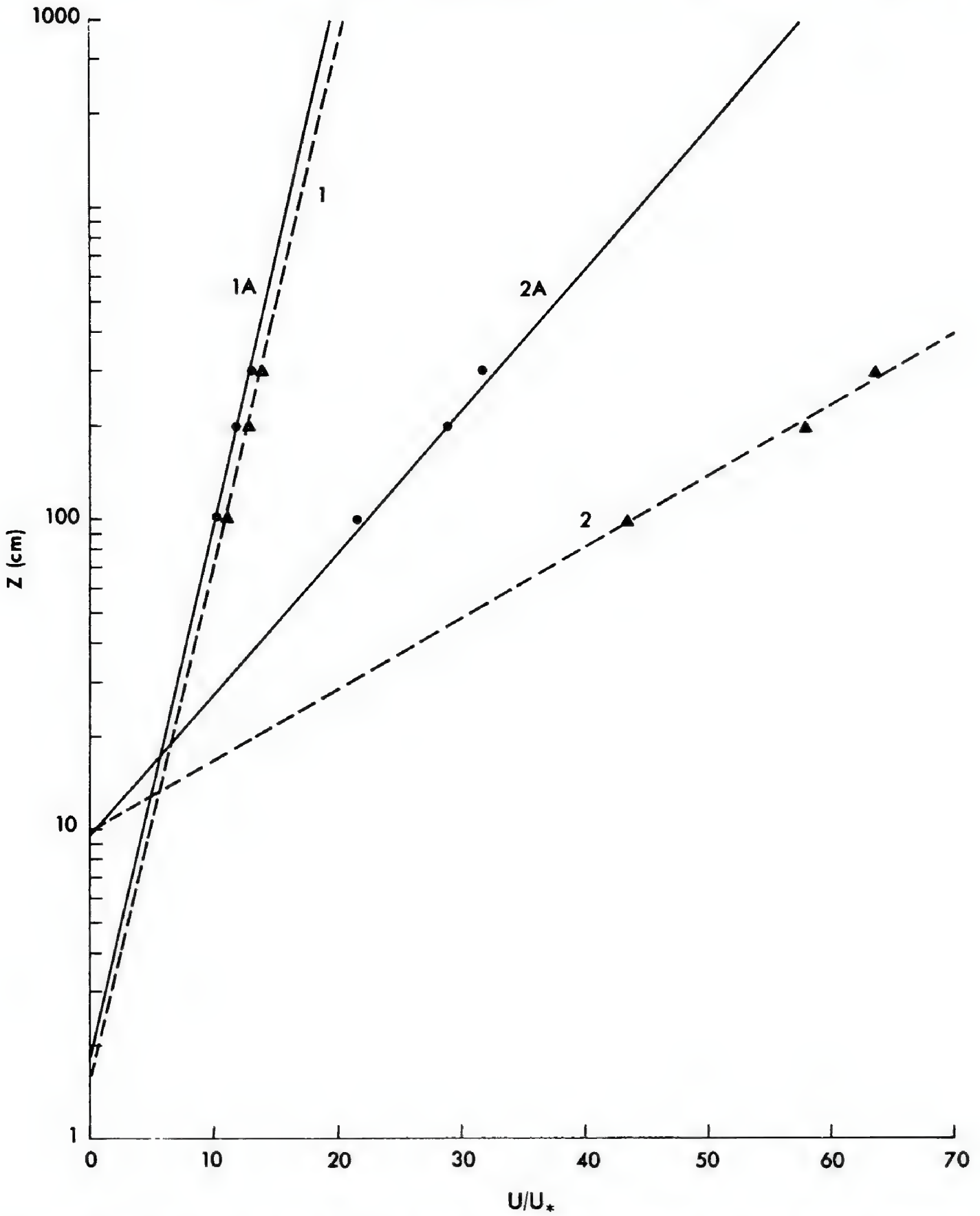


FIG. 4. Dimensional (profiles 1 and 2) and nondimensional (profiles 1A and 2A) plots of vertical current shear for sediment-laden and sediment-free flows (from Adams, submitted).

the flow during this period. The average value of the long-isobath wind stress component from Figure 1 is $\tau_w \cong \tau_o \cong 3.5$ dynes or $u_* = 1.9$ cm s$^{-1}$. The data of McCave (1971; Fig. 13) indicate that 3.5$\phi$ particles will move as suspended load when $u_* \geqq 1.3$ cm s$^{-1}$. Thus during this period current effects alone are adequate to resuspend the coarser sand-sized sediments found at the site. It should be noted that $\tau_o$ calculated from the assumption of

a frictional boundary layer yields a value that is about 20% smaller than the value calculated from Equation (1).

The velocity data of profile 2, nondimensionalized by the reduced $u_*$, are plotted as profile 2A (Fig. 4). The dimensionless profiles (1A, 2A) are similar to those found by others (Vanoni and Nomicos 1959, McCave 1973, Adams and Weatherly 1981a) who have sought to contrast the velocity structures of sediment-laden and sediment-free flows. The combinations of high bottom stresses and eastward flow during the period 2794 hr $\leqq t \leqq$ 2805 hr suggests that sand-sized and finer sediments are being transported to the east during this flow event.

## DISCUSSION AND CONCLUSIONS

From more than 4 months of current profile data it has been possible to characterize the flow in the bottom boundary layer and to make inferences concerning sediment transport processes during the winter at a location offshore of the developing Atchafalaya River delta. A distinctive feature of the data record is the presence of eight separate periods during which the bottom stress (calculated from Equation (1) ) exceeded the critical stress required to place 3.5$\phi$ sediment in suspension. Seven of those suspension events were characterized by flow to the east, and two (January 20 and February 24, 1979) likely were of sufficient intensity ($\tau_o \geqq 3.5$–$4.5$ dynes cm$^{-2}$) to cause significant bottom scour. The magnitude of the transport and deposition processes induced by one or both of these intense events is suggested by the observations of the depth of burial (0.5 m) of the legs of the instrument platform (see above).

A further indication of sediment resuspension comes from a comparison of velocity profile data from two different flow regimes during the period February 22–26, 1979. The earlier part of this record represents tidally dominated flow which is competent to erode only the silts and clays present. This earlier period is, to a large extent, representative of the mean flow during the entire 4½-month period. The later regime consists, in part, of the wind-driven easterly flow event (described above), which was of sufficient intensity as determined by two independent methods to erode the sand-sized material present. Insofar as the data examined represent mean conditions for the area of interest there are strong indications that sand-sized material is moved selectively to the east and therefore the bottom sediments west of the source area should be deficient in the coarser components. This is not inconsistent with the few observations of shelf sediment distribution that are available for this area.

As a device for examining the relative dispersion of sand-sized sediments in a quantitative manner, current vectors were progressively summed for each period during which $\tau_o \cong \tau_c = 1.7$ dynes cm$^{-2}$. In this case $\tau_o$ was computed from Equation (1) (see Fig. 3C). Further, it was assumed that, once in suspension, particles would remain in suspension until $\tau_o < 0.9\,\tau_c$. This progressive transport vector diagram is shown in Figure 5. The

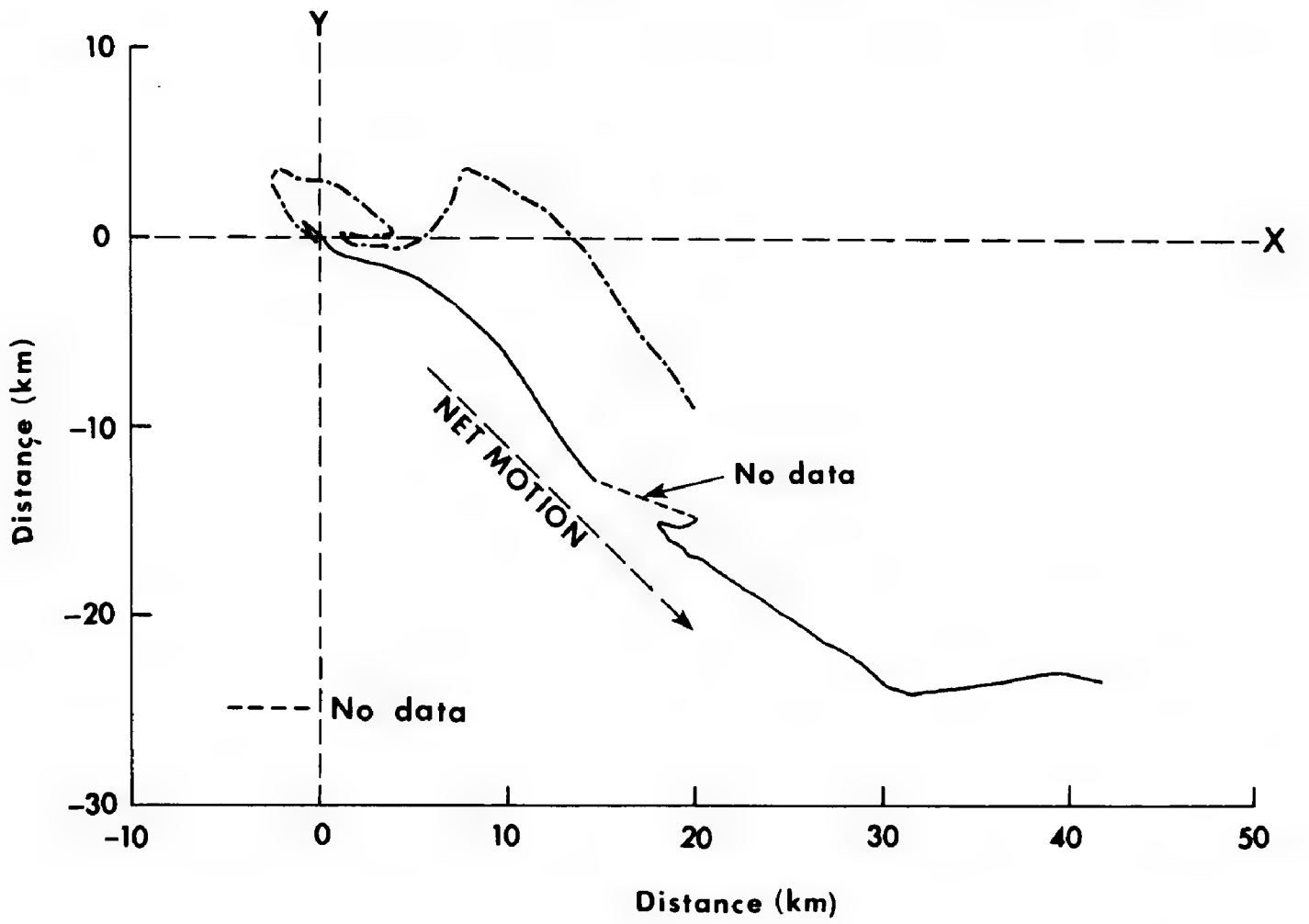


FIG. 5. Progressive transport vector plot of sediment displacement at the 1-m level for the period November 1, 1978, to March 12, 1979. The dashed line is based on combined current and wave stress.

coordinate system is the same as in Figure 2. Wind data indicate that movement of the sand-sized component during the period January 23–28, 1979, when current meter data were not available, was nominally eastward. As might be expected, the inclusion of bottom stress generated by wave motion results in sediment being moved farther to the east, although the difference is less than might be expected. In either case, qualitatively the results are the same, *i.e.,* an eastward alongshore motion of about 40 km and an offshore displacement of about 20 km. This is in marked contrast to the water displacement (Fig. 2) as inferred from the 1-m current meter, which gives a westward and onshore displacement of about 200 km and 150 km, respectively. Thus current meter data, even from very near the bottom, in the absence of information concerning local bottom sediments and resuspension criteria, may be a very poor indicator of sediment motion and dispersion. It is important to note that the analysis does not consider the effects of major storms on the distribution of sediment. It is quite likely that a large storm (a hurricane, for example) would completely obliterate the sediment distribution patterns created by the normal flow patterns. Major storms, however, are sufficiently infrequent so that their effects are not likely to be dominant over a time scale of a few decades or longer.

The rate and manner of growth of the Atchafalaya River delta onto the continental shelf depends to a great extent on the nature and the quantity of

sediment available for delta progradation. According to Garrett *et al.* (1969), approximately $3 \times 10^{10}$ kg of sediment enters Atchafalaya Bay each year. This is about 10% of the sediment load carried by the Mississippi River. Sediments deposited in Atchafalaya Bay have changed from a dominance of silt and clay to silt and fine sand over the last 20 years (Roberts *et al.* 1980). Large volumes of sand reached the bay during the high-water years of 1973–1975, and Roberts *et al.* (1980) have suggested that much of this increase was related to scouring of previously deposited material. Data published from U.S. Army Corps of Engineers files shows that during recent years 25% of the total sediment load of the Atchafalaya River at the point of departure from the Mississippi River is sand and that 90% of this sand enters Atchafalaya Bay through the Wax Lake and lower Atchafalaya River outlets. Although exact percentages of sand-sized material leaving the bay are unknown, quantities probably are now substantial and should increase with time as the bay fills. The foregoing analysis suggests that much of the sand-sized material that reaches the shelf will be redistributed in winter by winds associated with cold-front passages. Moreover, the path of redistribution by these processes should be principally to the east and offshore.

The observational data needed for estimating suspended sediment concentrations in the water column are not available. Quantitative estimates of sediment transport rates associated with the described currents thus cannot be made. It is clear, however, that bottom stresses associated with frontal passages (and the accompanying surface waves) are adequate to resuspend substantial quantities of bottom sediments. This resuspended material then may be transported by the wind-driven mean flow in an easterly direction. Following a frontal passage, the flow regime again becomes dominated by rotary currents and diminished wave activity, which result in a net westerly drift. The mean rotary currents, however, are incompetent to resuspend sands or coarse sediments or to retain in suspension those coarse materials that were picked up during the period of high winds and waves. Thus there is a potential for a net transport to the east of the coarser materials present. The occurrence of 15–20 of these easterly flow events during a normal winter may exert a significant influence on the distribution of sediments locally and possibly on the gross distribution of sediments associated with the delta developing on the shelf. The impact these processes will have on the Atchafalaya Delta which will soon express itself on the continental shelf is a subject for future research. Riverine processes causing progradation will need to be balanced against redistribution processes in the receiving basin such as winter cold fronts, wave-induced longshore drift, violent storms, and others. However, in the absence of long-term sediment studies it is unclear how these flow events influence the overall sediment budget on the Louisiana shelf.

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## LITERATURE CITED

ADAMS, C. E. and G. L. WEATHERLY. 1981a. Some effects of suspended sediment on an oceanic bottom boundary layer. *Journal of Geophysical Research.* 86:4161–4172.

_____ and _____. 1981b. Suspended sediment transport and benthic boundary layer dynamics. *Marine Geology.* 42:1–18.

BAGNOLD, R. A. 1966. An approach to the sediment transport problem from general physics. *Professional Papers, U.S. Geological Survey. No.* 422I, 37 pp.

BROWER, W. A., J. M. MESERVE and R. G. QUAYLE. 1972. Environmental guide for the U.S. Gulf Coast. Prepared for U.S. Army Corps of Engineers by National Oceanic and Atmospheric Administration, EOS, NCC, Asheville, N.C., 177 pp.

DADDIO, E., W. J. WISEMAN, JR. and S. P. MURRAY. 1978. Inertial currents over the inner shelf near 30°N. *Journal of Physical Oceanography.* 8:728–733.

FISK, H. N. 1952. Geological investigations of the Atchafalaya Basin and the problem of Mississippi River diversion. U.S. Army Corps of Engineers, Mississippi River Commission, Vicksburg, MS, Vol. 1, 145 pp.

FRAZIER, D. E. 1967. Recent deltaic deposits of the Mississippi River: their development and chronology. *Transactions of the Gulf Coast Association of Geological Societies.* 17:287–311.

FREY, H. R. and G. F. APPELL (eds). 1981. NOS Strategic Petroleum Reserve Support Project: Final Report, Vol. 2—Measurements and Data Quality Assurance. U.S. Dept. of Commerce, National Oceanic and Atmospheric Administration, National Ocean Survey.

GRANT, W. D. and O. S. MADSEN. 1979. Combined wave and current interaction with a rough bottom. *Journal of Geophysical Research.* 84:1797–1808.

GARRETT, B. J., P. HAWXHURST and J. R. MILLER. 1969. Atchafalaya Basin, Louisiana, lower Atchafalaya River and Wax Lake Outlet. U.S. Army Corps of Engineers, New Orleans District, 66th Committee on Tidal Hydraulics Conference.

HAUSKNECHT, K. A. 1980. Biological/chemical survey of Texoma and Capline sector salt dome brine disposal sites off Louisiana. *Work Unit 3.1, Sediments and Suspended Particulates, Final Report,* 56 pp., Energy Resources Co., Inc., Cambridge, Mass.

HUYER, A., R. S. SMITH and E. J. C. SOBEY. 1978. Seasonal differences in low frequency current fluctuations over the Oregon continental shelf. *Journal of Geophysical Research.* 83:5077–5089.

McCAVE, I. N. 1971. Sand waves in the North Sea off the coast of Holland. *Marine Geology.* 10:199–225.

_____. 1973. Some boundary-layer characteristics of tidal currents bearing sand in suspension. *Memoires de la Societe Royale des Sciences de Liege.* 6 ser., 6:187–206.

MURRAY, S. P. 1976. Currents and circulation in the coastal waters of Louisiana. *Sea Grant Publication No.* LSU-T-76-003. 33 pp.

NIHOUL, J. C. J. 1977. Turbulent boundary layer bearing silt in suspension. *Physics of Fluids.* 10:197–203.

OWEN, M. W. 1977. Problems in the modeling of transport, erosion and deposition of cohesive sediments. In E. G. Goldlberg *et al.* (eds.) *The Sea,* Vol. 6. Wiley Interscience, N.Y.

ROBERTS, H. H., R. D. ADAMS and R. H. W. CUNNINGHAM. 1980. Evaluation of sand-dominant subaerial phase, Atchafalaya Delta, Louisiana. *Bulletin, American Association of Petroleum Geologists.* 64:264–279.

SMITH, J. D. 1977. Modeling of sediment on continental shelves. In E. D. Goldberg *et al.* (eds.) *The Sea,* Vol. 6. Wiley Interscience, York.

_____ and S. R. McLEAN. 1977. Boundary layer adjustments to bottom topography and suspended sediment. In J. Nihoul (ed.) *Bottom Turbulence,* pp. 123–151. Elsevier, New York.

SMITH, N. P. 1977. Near-bottom cross-shelf currents in the northwestern Gulf of Mexico; a response to wind forcing. *Journal of Physical Oceanography.* 7:615–620.

VAN HEERDEN, I. LL. and H. H. ROBERTS. 1980. The Atchafalaya delta—Louisiana's new prograding coast. *Gulf Coast Association of Geological Societies.* 30:497–506.

VANONI, V. A. and G. N. NOMICOS. 1959. Resistance properties of sediment-laden streams. *Journal of the Hydraulics Division, ASCE.* 85(HY5):77–107.

WINANT, C. D. and R. C. BEARDSLEY. 1979. A comparison of shallow currents induced by wind stress. *Journal of Physical Oceanography.* 9:218–220.

*Contributions in Marine Science.* (1982) Vol. 25:149–159.

# DISSOLVED BARIUM IN SOME LOUISIANA OFFSHORE WATERS: PROBLEMS IN ESTABLISHING BASELINE VALUES

Lui-Heung Chan and Jeffrey S. Hanor

*Department of Geology, Louisiana State University, Baton Rouge, Louisiana 70803*

## ABSTRACT

Dissolved barium values in samples of Louisiana offshore waters collected during the Gulf Universities Research Consortium—Offshore Ecology Investigation range from 31 to 67 μg/kg in waters of chlorosities of 11 to 19 g/l. The barium values are higher than normal open Gulf of Mexico values (11–12 μg/kg) and are in excess of those reasonably expected from conservative mixing of Mississippi River and Gulf waters. It is possible that some of this excess barium is the result of the discharge of effluents from offshore drilling platforms. Much of it, however, can probably be accounted for by simple desorption of barium from river-borne suspended material during natural processes of estuarine mixing. Additional work is required to quantify the relative contributions of natural and anthropogenic sources of barium.

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## INTRODUCTION

The distribution of dissolved barium in Louisiana coastal waters is of special interest because of the likelihood that excess barium has been and is being introduced into the marine environment as a result of development of Louisiana's offshore petroleum resources. Barite drilling mud and high-barium formation waters (White, Hem and Waring 1963; Hanor and Baria 1977) are both potential sources of excess barium. Jones and Williams (1979), in a study of the composition of bottom sediments in Timbalier Bay and adjacent offshore areas, have attributed high barium concentrations they found in some of these sediments to the introduction of barite from drilling mud. Other workers have also noted the presence of apparent barium anomalies in offshore sediments of the Gulf Coast and have suggested industrial sources (*e.g.*, Wheeler, Anderson, Schwarzer and Hokanson 1980). The possibility exists, therefore, that the distribution of barium could be used to determine the magnitude of industrial input and the direction and rate of dispersal of platform effluents.

While some information exists on the barium levels in offshore Louisiana sediments, no previous studies have been published on the distribution of dissolved barium in the overlying coastal waters. Chow (1976) has measured the dissolved barium content of some coastal waters off Southern California

and has suggested that this element can be used as a tracer for drilling-related contamination of seawater. Successful application of this concept, however, requires prior knowledge of what the natural, base-line values for dissolved barium are in a particular coastal environment. What constitutes an anomaly? What range of values can be accounted for simply by natural processes of mixing and sediment-water interaction?

The purpose of this paper is to present the first published information on the levels and variability of dissolved barium in Louisiana coastal waters and to discuss problems which should be addressed in future work in establishing natural baseline levels for barium.

## STUDY AREA

During the period of 1972 to 1974, the Gulf Universities Research Consortium (GURC) conducted the Offshore Ecology Investigation (OEI) to study the effect of drilling and production on the Louisiana coastal environment (Wards, Bender and Reish 1979). We were asked by GURC to determine dissolved barium in a suite of offshore water samples collected from the Timbalier and Barataria Bay area of the Louisiana Gulf coast, immediately to the west of the Mississippi River delta (Figure 1).

Waters in the study area represent a blend of at least three different sources: 1) coastal fresh water discharged seaward through the Barataria and Timbalier estuarine complexes, 2) Mississippi River water swept westward by surface currents, and 3) marine water of the open Gulf. At the time of sampling, April 1973, the Mississippi River was in flood stage, and much of the fresh water input into the study area was presumably from this source. The GURC-OEI sampling plan did not include obtaining samples from the three end-members. Because we were invited to participate in the program three months after sampling had been completed it was not possible for us to go back and obtain suitable end-member samples.

The water samples we analyzed were collected on April 4 and 6, 1973 from stations along GURC-OEI transects. Figure 2 shows the location of the stations relative to the position of offshore platforms in the study area. Table 1 gives coordinates and water depths for each sample. All samples except GSRI-516, were from stations located away from high concentrations of offshore platforms.

## ANALYTICAL TECHNIQUES

The water samples used in this study were supplied by the Gulf South Research Institute, (GSRI), and we were not directly or indirectly involved in either the planning or sampling phase of the investigation. The samples we received were unfiltered, but had been treated with 5 ml of concentrated $HNO_3$ per liter of sample. This is a potentially undesirable procedure which could result in the release of barium from exchange sites or lattice sites in suspended particulate matter. However, for reasons that we will develop, we believe that these potential sources of error are probably of secondary importance and that our data as a group provide useful information on the distribution of barium in the study area.

The samples were filtered in our laboratory through 0.45 μm Millipore membranes and analyzed for barium and chloride in August 1973. Barium was determined by a high precision method of mass-spectrometry isotope-dilution (Chan, Drummond, Edmond and Grant 1977). An aliquot of filtered water sample was spiked with a known quantity of Ba-135. Barium was separated from other dissolved salts by ion exchange chromatography using a Dowex 50 W x 8 resin column. The barium fraction was mounted on a pre-baked tantalum filament and the isotopic ratio, Ba-135 / Ba-138, was measured in a 90° sector, 12-in, radius mass spectrometer. This technique gives an analytical precision of 0.7% and an accuracy of 1%.

Chloride was determined by the standard Mohr titration method.

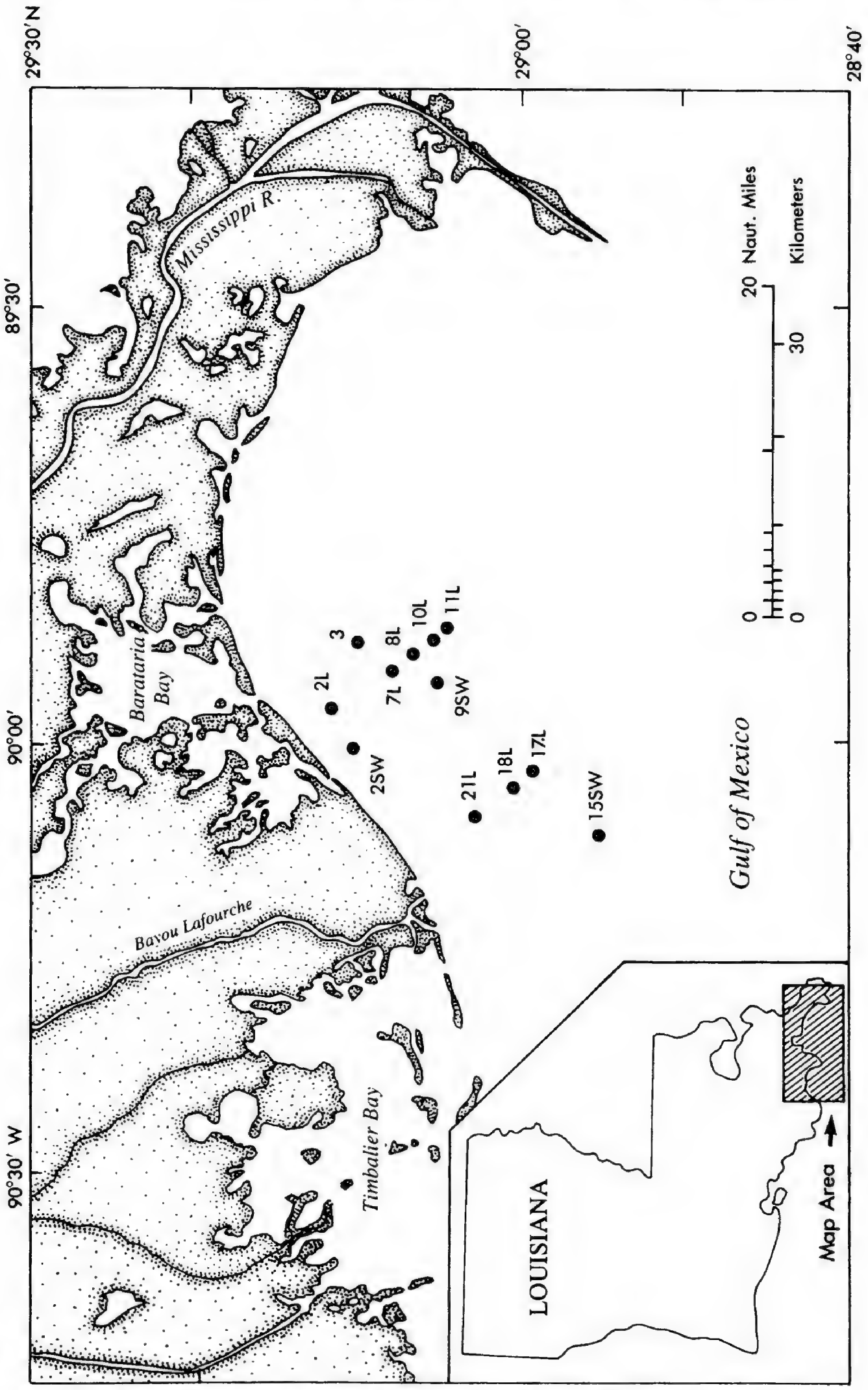


FIG. 1. Map showing study area of the Louisiana Gulf coast. Solid circles indicate sampling stations.

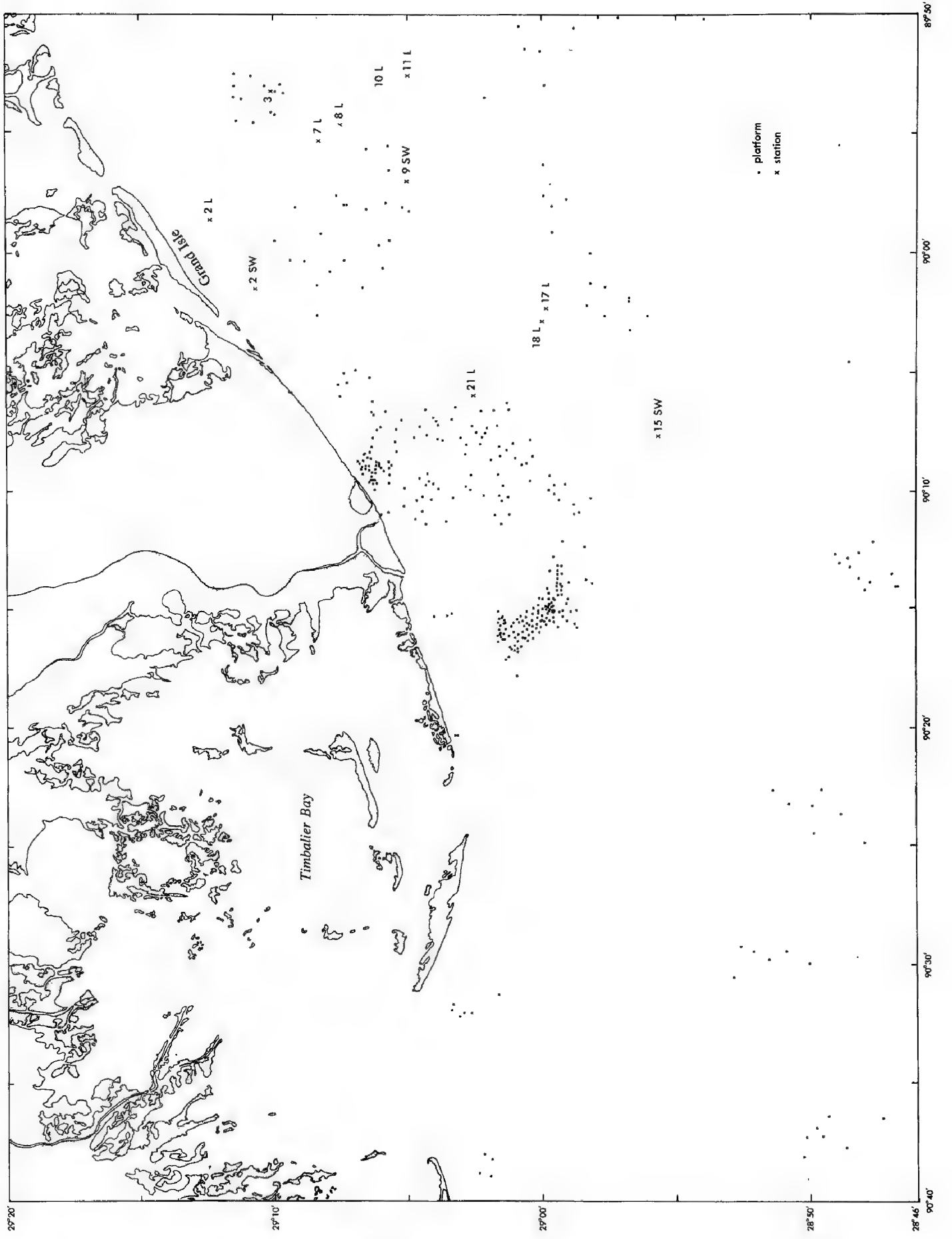


FIG. 2. Locations of sampling stations relative to the positions of drilling platforms in the northern Gulf of Mexico.

TABLE 1

**Concentrations of chloride and barium in Louisiana offshore waters, April 4 and 6, 1973.**

| Station | Location | | Water Depth m | GSRI Sample Number | Cl g/l | Ba µg/kg |
|---|---|---|---|---|---|---|
| | Latitude N | Longitude W | | | | |
| 2SW | 29°10.60' | 90°01.50' | 0 (S) | 513 | 11.8 | 51.4 |
| | | | 7 (B) | 511 | 14.3 | 56.3 |
| | | | 8 (B) | 502 | 14.4 | 55.2 |
| 2L | 29°12.39' | 89°58.63' | 11 (B) | 503 | 15.4 | 46.5 |
| 3 | 29°10.00' | 89°53.25' | -- (I)[1] | 516 | 12.8 | 66.8 |
| 7L | 29°08.31' | 89°55.28' | 13 (B) | 514 | 17.7 | 23.1 |
| 8L | 29°07.50' | 89°54.59 | 0 (S) | 509 | 11.6 | 56.2 |
| 9SW | 29°05.00' | 89°56.80' | 12 (B) | 508 | 18.2 | 30.9 |
| 10L | 29°05.89' | 89°53.25' | 23 (B) | 517 | 18.6 | 40.4 |
| 11L | 29°05.06' | 89°52.56' | 0 (S) | 515 | 11.6 | 62.8 |
| | | | 25 (B) | 506 | 17.5 | 31.2 |
| 15SW | 28°55.70' | 90°07.70' | 21? | 501 | 10.9 | 55.9 |
| 17L | 28°59.67' | 90°02.84' | 0 (S) | 510 | 11.5 | 64.2 |
| 18L | 29°00.39' | 90°03.62' | 14 (I) | 505 | 14.0 | 40.1 |
| 21L | 29°02.56 | 90°06.00' | 9 (I) | 507 | 12.6 | 59.4 |

S = Surface water

I = Intermediate water

B = Bottom or near bottom water

[1] Water depth not given but deduced from chloride value.

## RESULTS

Analytical results are given in Table 1. Figure 3 shows the areal variation in dissolved barium and chloride in the surface waters and in the near-bottom waters of the study area. The chlorosity of the surface waters is quite uniform (Cl = 11.5 to 11.8 g/l), and increases slightly toward shore. There is a progressive increase in barium values, however, away from the Barataria Bay estuarine complex (51.4 µg/kg) and toward the Gulf (64.2 µg/kg) where the influence of the Mississippi River plume is more dominant.

The lateral variation in the composition of the bottom waters is more

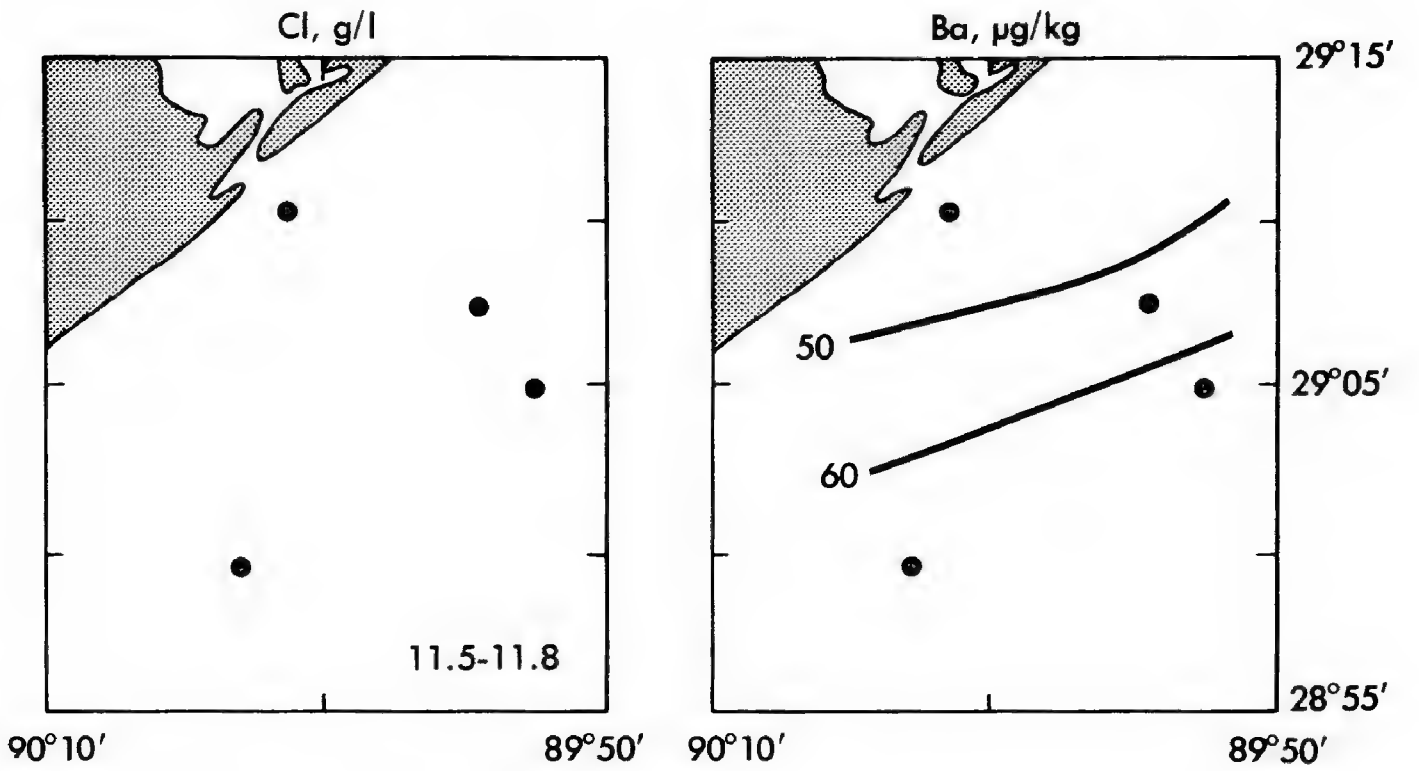


FIG. 3. Areal variation in dissolved chloride and barium in the surface waters and the intermediate and bottom waters of the study area. Contours are intended to show generalized trends only.

pronounced than in the surface waters. Chlorosity increases seaward from nearshore values of 14–15 g/l to offshore values approaching those of open sea water (18.6 g/l). Barium concentrations, in contrast, decrease by a factor of nearly two.

Figure 4 shows a plot of dissolved barium versus dissolved chloride for the GURC-OEI samples. Also shown is our estimate of the barium concentration

of open Gulf waters and a probable range in barium values for Mississippi River water, all based on our earlier analytical study of the behavior of dissolved barium in the Mississippi River estuary (Hanor and Chan 1977).

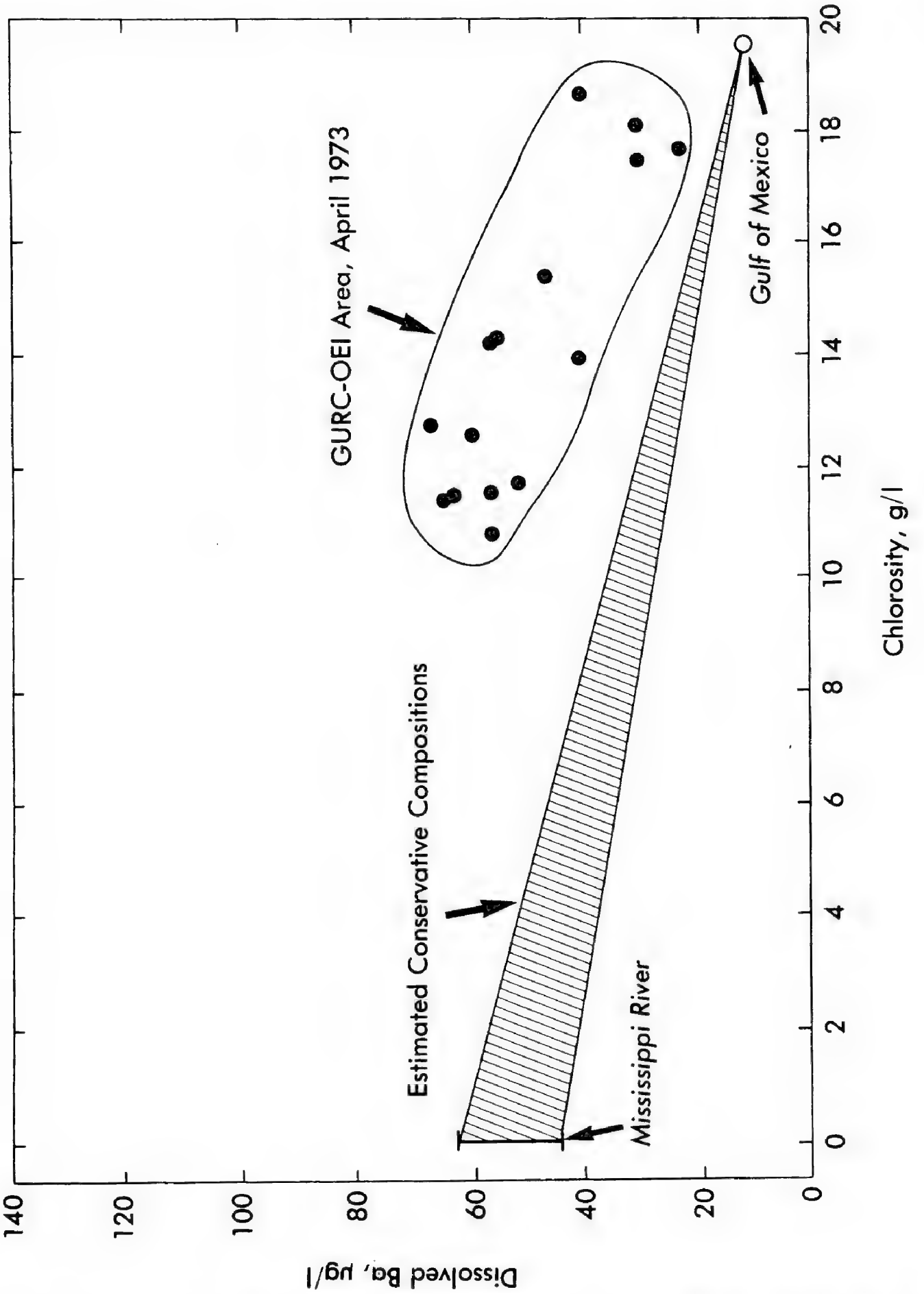


FIG. 4. Plot of dissolved barium versus chlorosity for Louisiana offshore waters, April, 1973. Also shown is the estimated composition that would result from conservative mixing of Mississippi River and Gulf of Mexico waters.

## DISCUSSION

From a cursory examination of Figure 4, a scatter plot of barium versus chloride for the GURC-OEI samples, it might be possible to conclude that Louisiana coastal waters contain anomalously high levels of dissolved barium. All of the barium values are in excess of barium values that would be expected from conservative mixing of Mississippi River and Gulf of Mexico waters. The barium concentration of water discharged from the Timbalier and Barataria estuarine complexes are not known, but for reasons we will discuss, are probably lower than those in the end-member Mississippi River water.

Are the excess barium values in fact anomalous values? We think alternative explanations are possible. In an earlier paper (Hanor and Chan 1977), we discussed the results of a study of the behavior of dissolved barium in the Mississippi River salt wedge estuary. Barium is transported downriver into the estuary both as dissolved ions and as ions adsorbed on suspended material. Because the ratio of major dissolved cations to dissolved barium is far greater in marine waters than in Mississippi River water, transport of suspended material through the salt wedge results in the quantitative stripping off of adsorbed barium by ion-exchange with major dissolved cations. Dissolved barium thus behaves in a strongly nonconservative manner, and the estuarine waters have dissolved barium concentrations far in excess of those which would be predicted by simple physical mixing of end-member River and Gulf waters.

Figure 5 shows a plot of dissolved barium versus dissolved chloride in the Mississippi River estuary for samples collected in October 1972. The solid curves represent predicted dissolved barium values assuming that exchange equilibrium is maintained between suspended load and the estuarine waters during mixing. Techniques for making these calculations are described in detail by Hanor and Chan (1977). At the time of sampling, end-member River and Gulf waters were found to contain 60 μg/l and 10 μg/l dissolved barium, respectively. The exchange curves are calculated for various assumed values of adsorbed barium entering the estuary.

Superimposed on the Mississippi River estuary analyses and the calculated ion-exchange/mixing curves are our observed values for barium in Louisiana coastal waters. As may be seen, most of the GURC-OEI samples fall within the range of values predicted by simple exchange and mixing for October 1972 waters. The values are higher than those which would result from conservative mixing. It is clear from our earlier work (Hanor and Chan 1977) that barium originally adsorbed on riverine suspended material can be a significant source of dissolved barium in coastal waters. Failure of the GURC-OEI sampling plan to include samples of end-member Mississippi River water and Timbalier-Barataria Bay estuarine waters in April 1973, however, precludes our being able to make a rigorous, quantitative analysis of the sources of dissolved barium in the Louisiana offshore waters. Our earlier study of October 1972 represents the Mississippi River at low stage. In

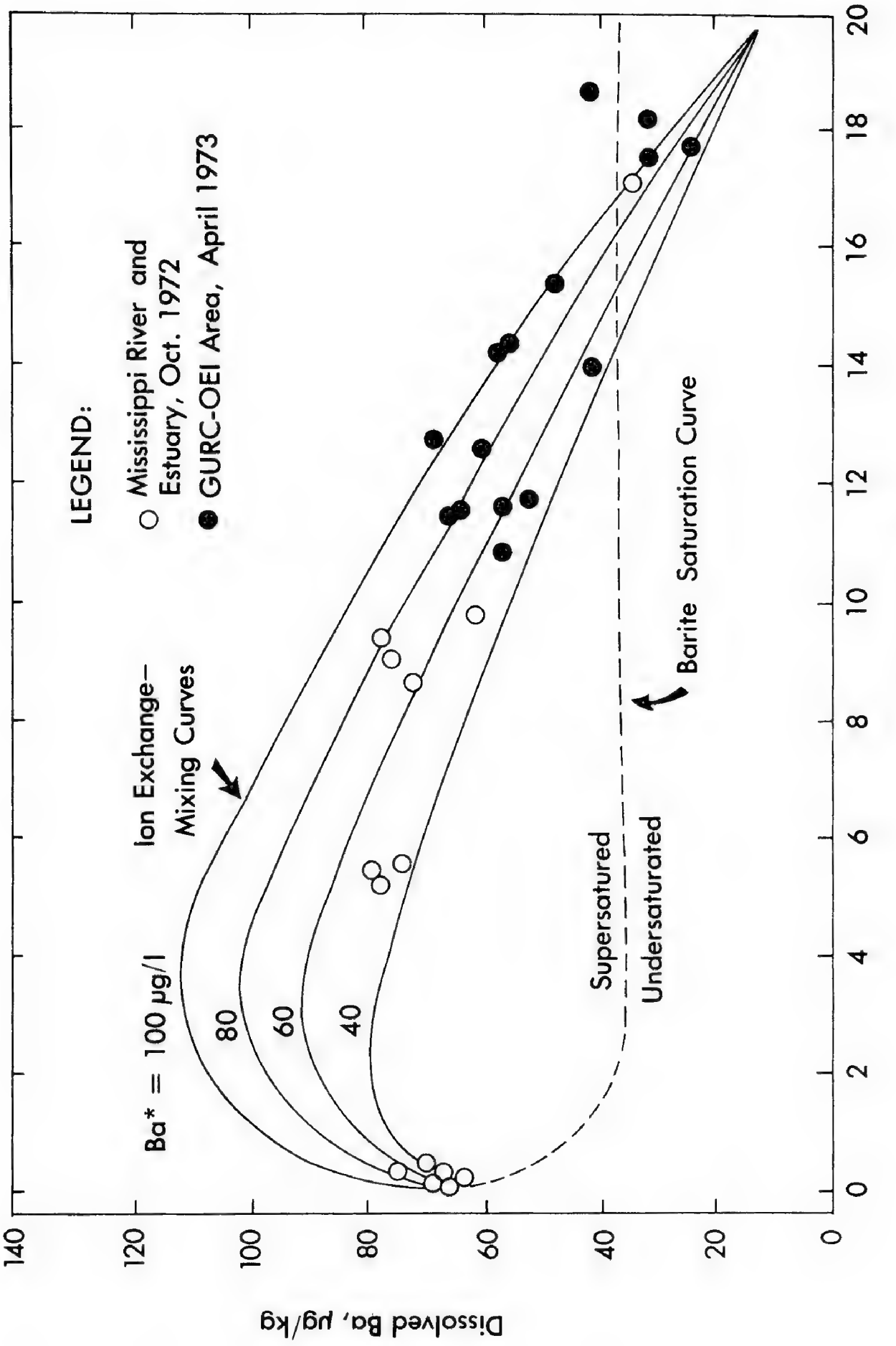


FIG. 5. Variation of dissolved barium as a function of chlorosity for the Mississippi River estuary waters, October, 1972 (open circles) and Louisiana coastal waters, April, 1973 (solid circles). Solid lines are calculated ion exchange curves for various values of adsorbed barium concentration (Ba*). Dashed line is the theoretical barite saturation curve.

April 1973, the River was at flood stage, and River end-member values for dissolved barium were probably lower than 60 μg/l (Durum and Haffety 1961). The input of adsorbed barium may have been greater, however, because of the greater concentrations of suspended material (Wells 1980) carried by the River at this time.

We do not know what the barium concentrations of Timbalier and Barataria Bay waters were at the time of sampling or whether exchange with suspended materials is an important process in these estuaries. The observation that barium values decrease shoreward in surface waters of nearly constant chlorosity (Figure 3) suggests that waters in these coastal estuarine complexes may have a lower barium concentration than waters discharged from the Mississippi River estuary to the east.

There is no evidence that saturation with respect to barite ($BaSO_4$) plays a significant role in controlling barium concentrations of the samples we analyzed. The dashed line in Figure 5 shows calculated concentration of barium in mixed waters in thermodynamic equilibrium with respect to pure barium sulfate. Techniques for making these calculations are given in Hanor (1969). Most of the waters represented in Figure 5 are apparently supersaturated with respect to barite. Although no studies have been made of barite nucleation in river and coastal waters, supersaturation levels of 14 to 58 times the equilibrium ion activity product for barium and sulfate are required to induce heterogeneous nucleation in experimental systems (Collins and Leineweber 1956). Higher supersaturation levels may be required for homogeneous precipitation (Blount 1974).

Of the GURC-OEI samples we analyzed, the sample from station 10 L appears to have a barium value in excess of that which can be reasonably accounted for by mixing and ion-exchange. Station 10 L is located in an area of low density of offshore platforms and drilling activity. Whether this barium value represents an artifact of sample treatment or is associated with effluents originating from platforms to the east cannot be ascertained at this time.

## CONCLUSIONS

The concentration of dissolved barium in Louisiana coastal waters appears to be anomalously high relative to concentrations expected from simple mixing of Mississippi River and Gulf of Mexico waters. While one might initially ascribe the presence of this apparent anomaly to the discharge of effluents from offshore drilling platforms, we now recognize that excess barium can also be introduced by desorption from river-borne clays during the natural processes of mixing.

Although the relative contributions of natural and industrial inputs of barium into Louisiana offshore waters cannot be resolved on a quantitative basis by the present data, our preliminary study does demonstrate that the geochemistry of coastal waters of intermediate salinity cannot be studied as a self-contained and independent system. To understand compositions and

to evaluate anthropogenic perturbations, it is necessary to consider processes which occur over the entire spectrum of mixing of fresh and marine waters. Future study of the controls on dissolved barium and other trace constituents in Louisiana offshore waters and similar coastal areas should include the characterization of 1) all end member water types and 2) the natural processes of adsorption, desorption, and precipitation that may occur when various waters and their suspended materials are mixed together. Without such information it will not be possible to establish baseline levels against which the existence of additional sources or sinks can be established.

## ACKNOWLEDGMENTS

We thank Dr. Donald V. Brady of the Gulf South Research Institute for providing us with the GURC-OEI water samples. Chloride analyses were performed by Maria Mostert.

## REFERENCES

BLOUNT, C. W. 1974. Synthesis of barite, celestite, anglesite, witherite and strontianite from aqueous solution. *American Mineralogist.* 59:1209–1216.

CHAN, L. H., D. DRUMMOND, J. M. EDMOND and B. GRANT. 1977. Barium distribution at the Atlantic GEOSECS station. *Deep-Sea Research.* 24:613–649.

CHOW, T. J. 1976. Barium in Southern California coastal waters, a potential indicator of marine drilling contamination. *Science.* 193:53–58.

COLLINS, F. C. and J. P. LEINEWEBER. 1956. Kinetics of the homogeneous precipitation of barium sulfate. *Journal of Physical Chemistry.* 60:389–394.

DURUM, W. H. and J. HAFFETY. 1961. Occurrence of minor elements in water. *Circular, U.S. Geological Survey.* No. 445. 11 p.

HANOR, J. S. 1969. Barite saturation in sea water. *Geochimica et Cosmochimica Acta.* 33:894–898.

_____ and L. R. BARIA. 1977. Controls on the distribution of barite deposits in Arkansas. In C. G. Stone (ed.) *Symposium on the geology of the Ouachita Mountains.* Ark. Geol. Comm., 42–49.

_____ and L. H. CHAN. 1977. Non-conservative behavior of barium during mixing of Mississippi River and Gulf of Mexico waters. *Earth and Planetary Science Letters.* 37:242–250.

JONES, J. I. and S. E. WILLIAMS. 1979. The distribution and origin of bottom sediments in Timbalier Bay, Louisiana and the adjacent offshore area, p. 201–222. In C. H. Wards, M. E. Bender and D. J. Reish (ed.) The Offshore Ecology Investigation: effects of oil drilling and production in a coastal environment. *Rice University Studies.* 65(4/5)589 p.

WARDS, C. H., M. E. BENDER and D. J. REISH (ed.) 1979. The Offshore Ecology Investigation: effects of oil drilling and production in a coastal environment. *Rice University Studies.* 65(4/5)589 p.

WELLS, F. C. 1980. Hydrology and water quality of the lower Mississippi River, Louisiana Dept. Transp. and Develop., Water Resources Tech. Rept. 21. 83 p.

WHEELER, R. B., T. B. ANDERSON, R. R. SCHWARZER and C. L. HOKANSON. 1980. Sedimentary processes and trace metal contaminants in the Buccaneer oil/gas field, Northwestern Gulf of Mexico. *Environmental Geology.* 3:163–178.

WHITE, D. E., J. D. HEM and G. A. WARING. 1963. Chemical composition of subsurface waters: *Professional Paper, U.S. Geological Survey. No.* 440-F. 67 p.

*Contributions in Marine Science.* (1982) Vol. 25:161–172.

# BOTTOM WATER OXYGEN CONCENTRATION IN THE MISSISSIPPI RIVER DELTA BIGHT

R. E. Turner and R. L. Allen

*Center for Wetland Resources, Louisiana State University, Baton Rouge, LA 70803-7507*

## ABSTRACT

Bottom water oxygen concentrations in the Mississippi River Delta Bight are commonly below saturation values. Hypoxic conditions (less than 3 $mg \cdot l^{-1}$) most often occur in shallow depths, west of the delta during summer. The hypoxic layer may be only a few meters thick and located on the bottom. An unusual midwater oxygen-depleted zone was observed south of Mobile Bay. The oxygen-minimum layer from deep water in the Gulf of Mexico *may* connect with low oxygen zones at the shelf break. *In situ* decomposition of material sinking from the surface layers is the most likely major oxygen consuming process. Lack of vertical mixing due to stratification probably contributes to the hypoxic summer conditions when oxygen concentration values are lowest.

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## INTRODUCTION

Knowledge of the oxygen distribution within continental shelf waters can be of assistance in understanding the biological oceanography of the shelf. Recent measurements of oxygen concentrations in the bottom waters of the northern Gulf of Mexico continental shelf have confirmed the existence of oxygen-deficient zones. There is an oxygen minimum layer (OML) beyond the continental shelf at a depth of 400 m depth (Richards and Redfield 1954), but it is not known if it enters shelf waters. Waters only partially satuated with oxygen have been reported to occur on the shelf by Ragan *et al.* (1978), Harper *et al.* (1981), and Bedinger *et al.* (1981) and at specific shallow nearshore zones (Fotheringham and Weissberg 1979; May 1973). The causal agents of these hypoxic zones are summarized by Gallaway (1981) to include the stratification and isolation of the bottom waters from surface waters, local oxygen sources and sinks, turbidity and organic loading from the Mississippi River sediments, and the residual effects of offshore oil and gas development. The effects on the biota are severe and result in a shift from '*k*' to '*r*'-strategy competition by the benthic community (*e.g.*, Santos and Simon 1980).

This study reports bottom oxygen concentrations taken during seven cruises in the Mississippi River Delta Bight and water column oxygen measurements from three cross-shelf transects. The objective was to

provide synoptic data in order to document the size of the hypoxic zones and to evaluate the factors influencing their formation.

## METHODS

The general sampling zone was in waters 8 to 100 m deep, from Mobile Bay on the east to the Atchafalaya River on the west. Three shelf transects were sampled for the vertical distribution of oxygen concentration: 20 km south of Mobile Bay, near Lake Pontchartrain, and south of Atchafalaya Bay (Fig. 1). Niskin bottles (2.5 l) were used to sample bottom water on seven cruises of the *R/V Oregon II* from March 1975 to November 1980. Though no bottom detection bottle-tripping device was employed, we gave careful attention to the hydro-wire tension and to the wire deployment relative to fathometer readings. These samples should, therefore, always have been collected within 3 m of the bottom. The Winkler titration method (Strickland and Parsons 1968) was used to calibrate temperature-compensated oxygen electrodes and for the direct determination of oxygen concentration of subsamples in 150 or 250 ml BOD bottles. Oxygen concentration profiles were made with a submersible oxygen probe equipped with a deck readout which included conductivity and temperature. Oxygen readings determined with the oxygen probe were corrected for differences in salinity between the calibration solutions and the *in situ* conditions. A Hydro-Products model 612 transmissometer was employed on one July cruise and calibrated to read 100% in distilled water. The instrument package was raised and lowered slowly and repeatedly to accurately delineate transition zones. A computer program was used to draw contour lines of equal oxygen concentration.

## RESULTS

The geographical distribution of oxygen concentration in the bottom waters east and west of the Mississippi River Delta is shown in Figure 2. In general, bottom waters were not oxygen-saturated and ranged from 3 to 7 mg oxygen·$l^{-1}$. The average oxygen concentration west of the river delta was equal to that east of the delta. Oxygen concentrations tended to decrease at the shelf break near the southern limit of our study area; the 100% saturation value at the shelf break was higher than inshore since water salinity increased and water temperature decreased offshore of the 50 m depth contour. Values lower than 2 mg oxygen·$l^{-1}$ occurred in shallow waters west of the delta during the summer (July) in both 1975 and 1976 and at only one station (March 1975) for the other cruises. One super-saturated value (10.4 mg·$l^{-1}$) occurred in November, 1980; but it is not known if this was due to incorrect titration, multiplication by the wrong constant, or sampling from an atypical area.

Oxygen concentrations along three transects in the summer are provided in Figure 3. Oxygen concentration decreased with depth along transects A and C. A narrow band of low-oxygen water, a few meters thick, which contained less than 4 mg oxygen·$l^{-1}$, was within 10 m of the bottom in transect A. Along transect C, this low-oxygen zone coincided with a turbid layer which extended offshore and which also enveloped a clearer, middle layer inshore.

In contrast there was no thin, low-oxygen bottom zone along the transect B beginning 20 km offshore of Mobile Bay; but there was a midwater layer of slightly lower oxygen concentration located at the thermocline. It contained a concentration of pink invertebrates, which could be seen with the unaided eye.

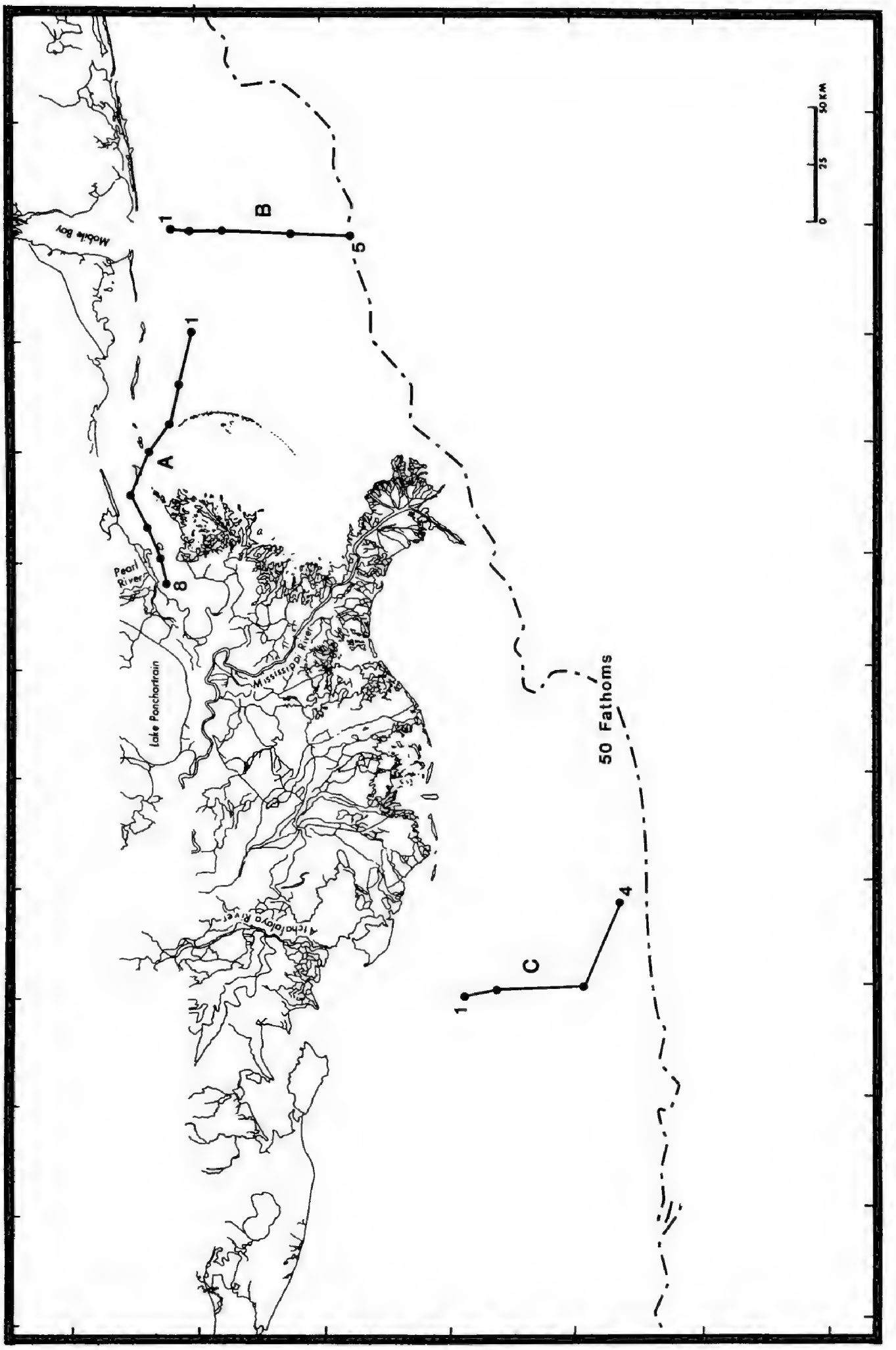



FIG. 1. The location of the sampling transects of July, 1976, and the general sampling area.

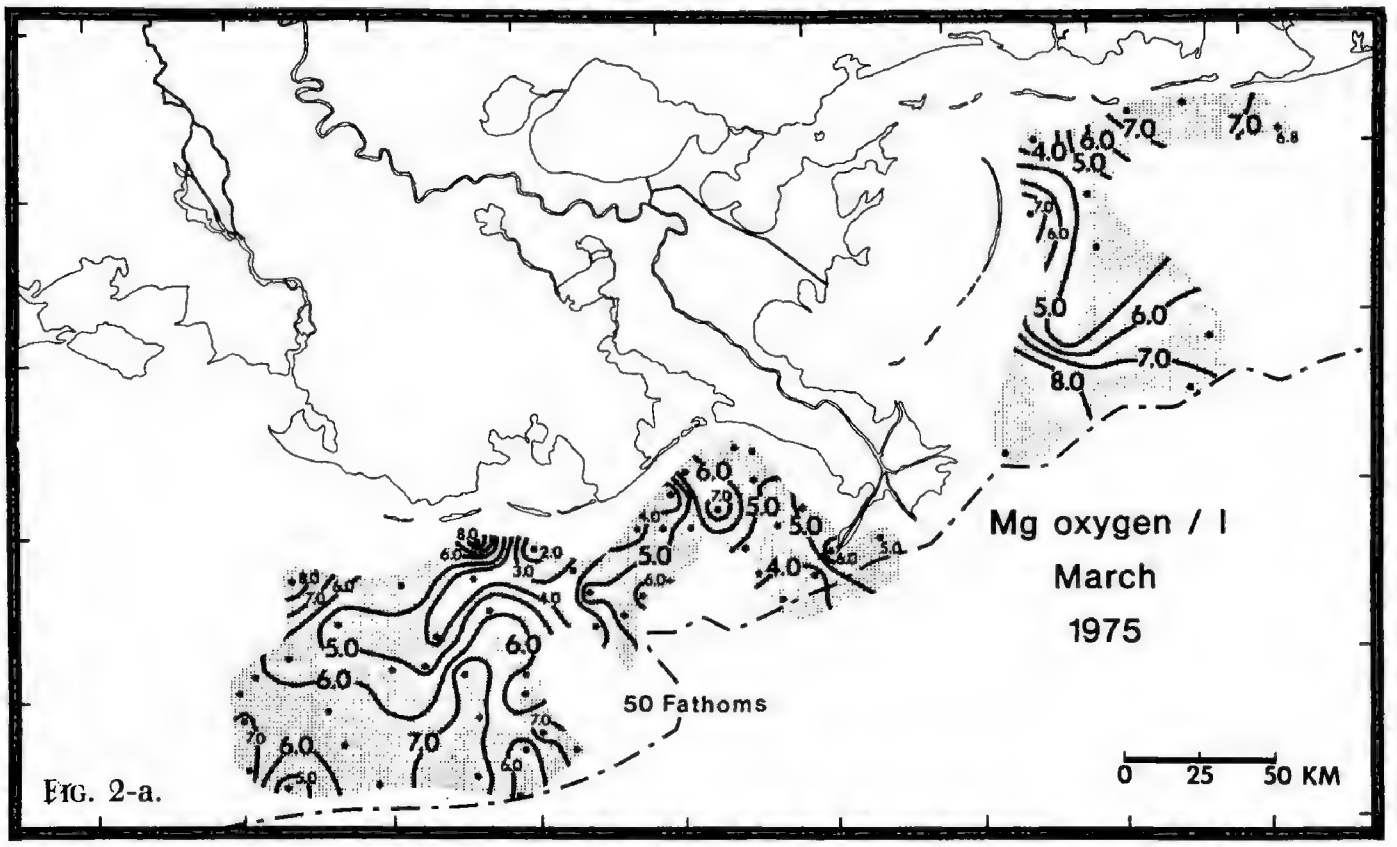



FIG. 2-a.

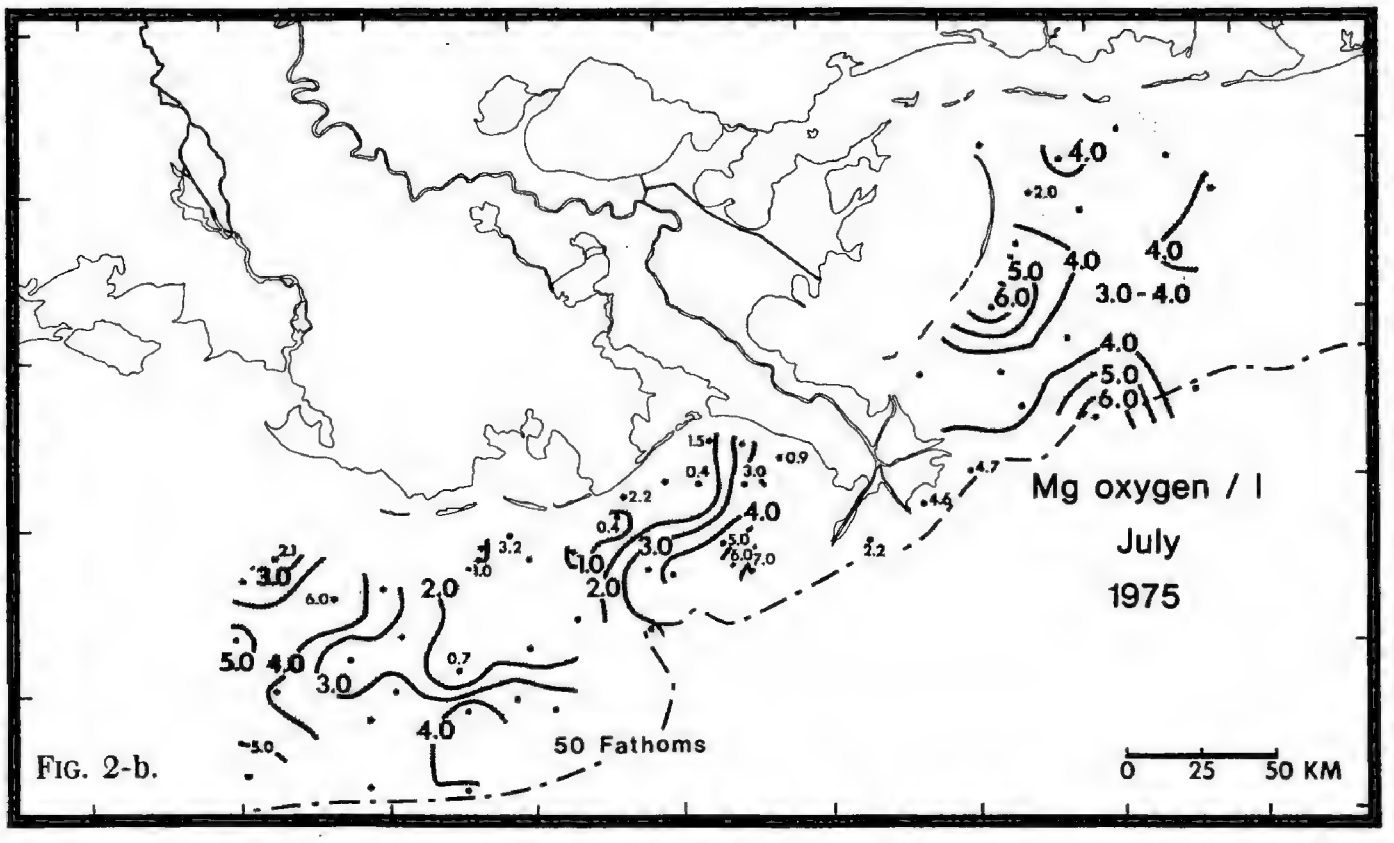



FIG. 2-b.

FIGS. 2 (a–g). Bottom oxygen concentrations (mg oxygen·l$^{-1}$) from seven cruises across the Mississippi River Delta Bight. The shaded area is the sampling zone.

## DISCUSSION

Oxygen concentrations in the bottom waters of this continental shelf usually appear to be below the saturation point. The concentration changes seasonally, and is lowest west of the delta in summer. Particularly low values of less than 3 mg·l$^{-1}$ are found in shallow, rather than in deep, waters. The

FIG.2-c.

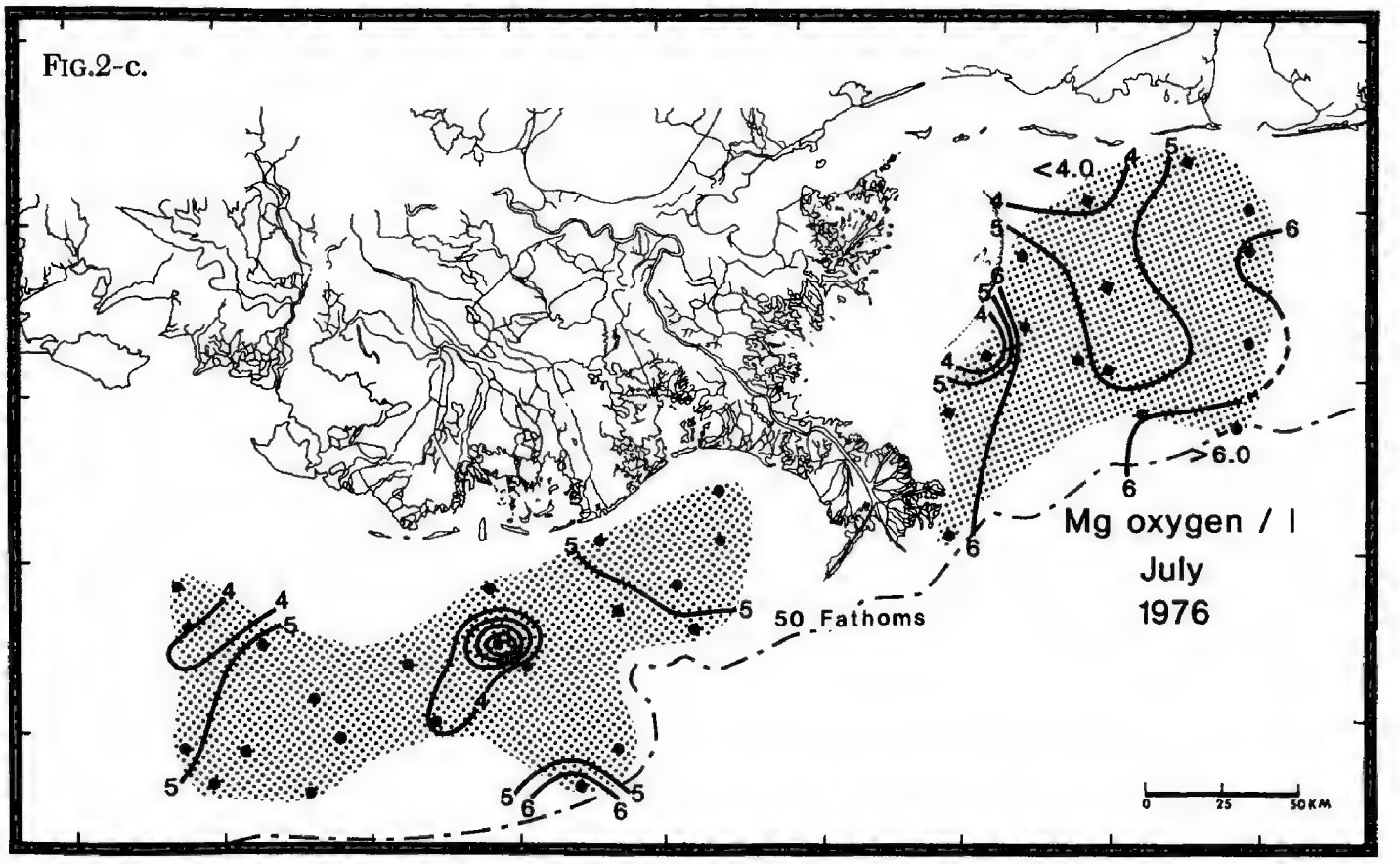
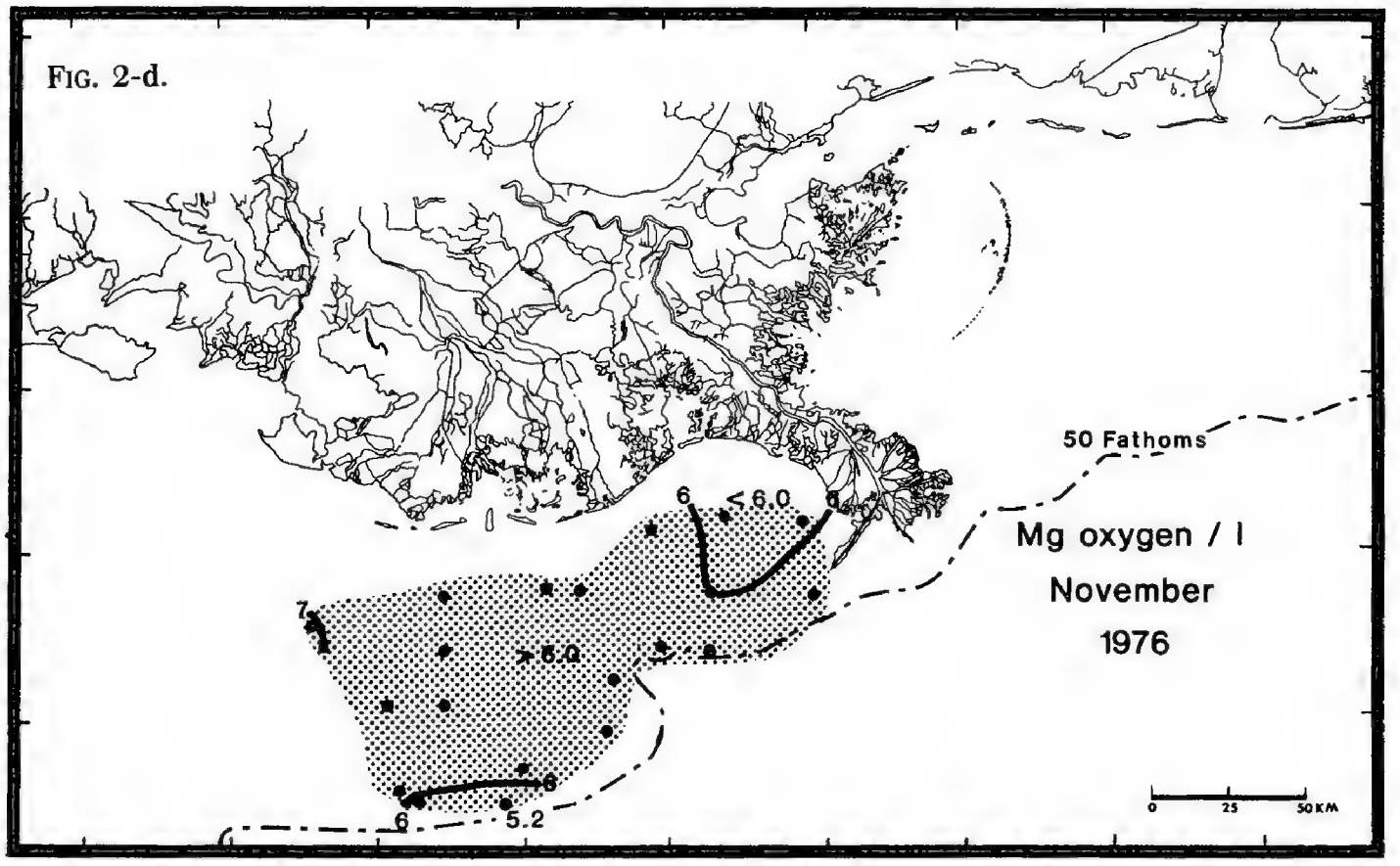



FIG. 2-d.




oxygen concentration and 100% saturation value along portions of the shelf decrease near the 50-ft contour and, therefore, may be indicative of some onwelling of mid-depth (400 m) waters of the oxygen minimum layer (OML) onto the shelf. Continuous vertical profiles of salinity, temperature, and density along cross-shelf transects support the possibility of such onwelling events (Turner and Allen, unpublished). The OML, however, contains at

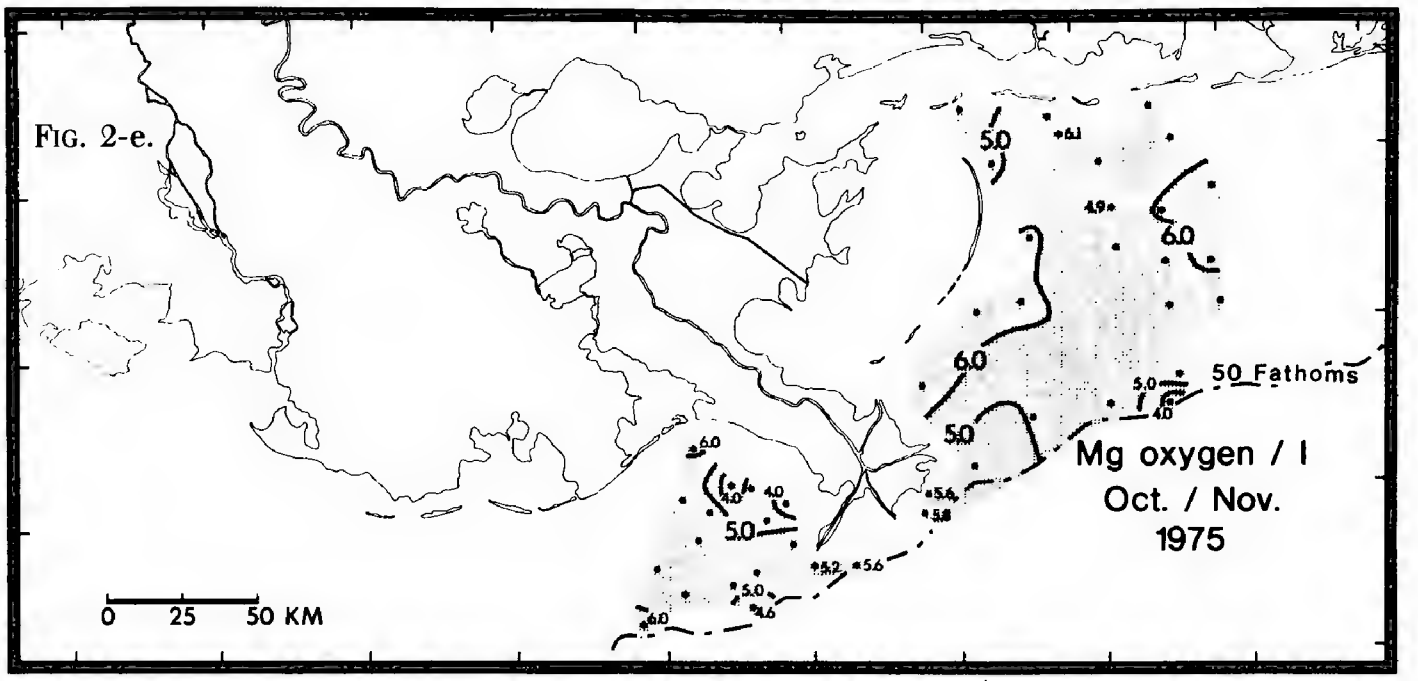



FIG. 2-e.

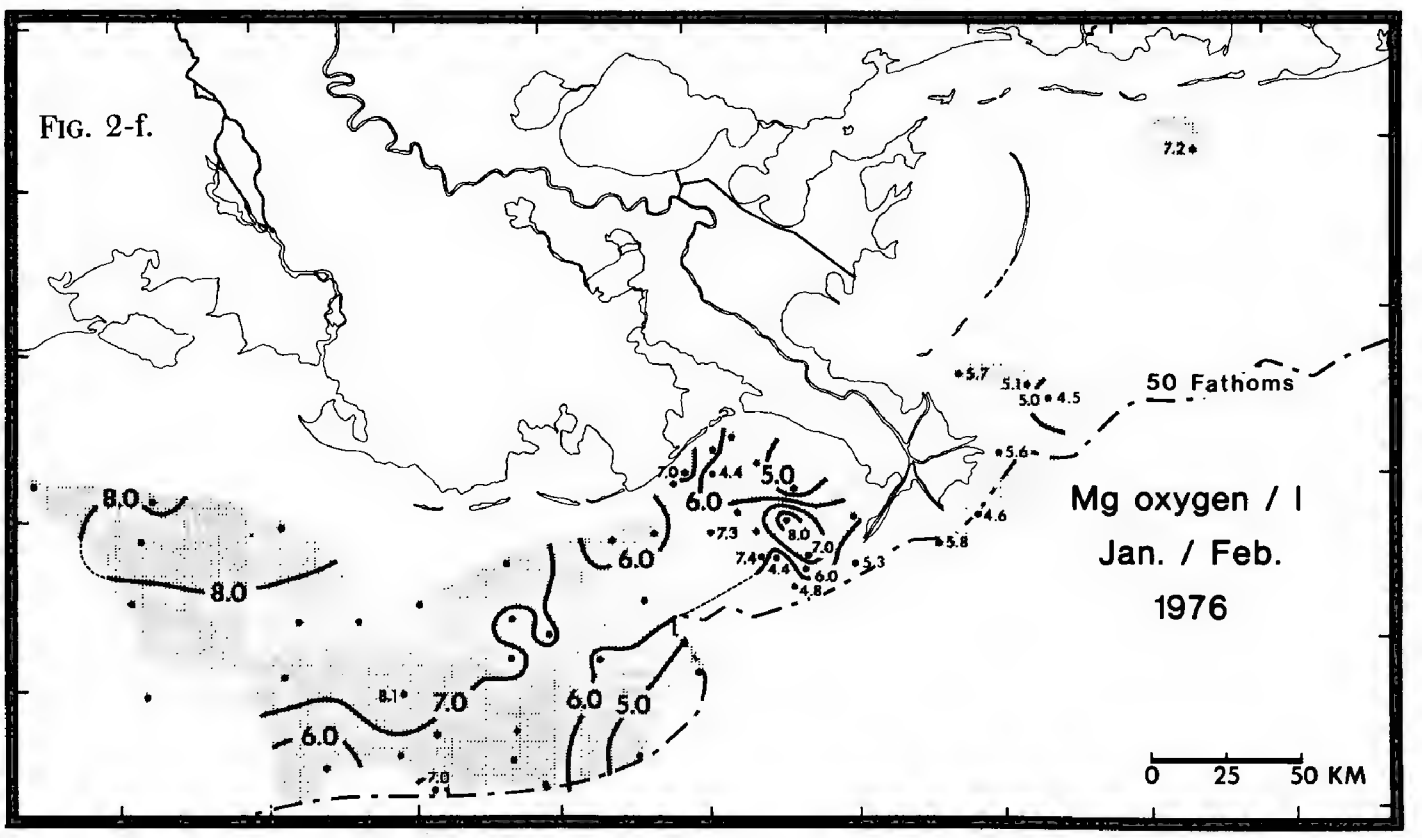



FIG. 2-f.

least 3.7 mg·l$^{-1}$. The lower oxygen concentrations found on the shelf during summer must therefore be the result of other, or additional, oxygen consuming processes. Since the oxygen concentrations tend to be higher immediately landward of the shelf break, *in situ* oxygen consumption, rather than onshore transport of the OML, seems to be the major relevant factor.

Both benthic and pelagic communities may consume dissolved oxygen in the benthic boundary layer. Sediments from the Mississippi River have been proposed as including important heterotrophic substrates which, upon consumption, may result in low-oxygen conditions (Gallaway 1981). The

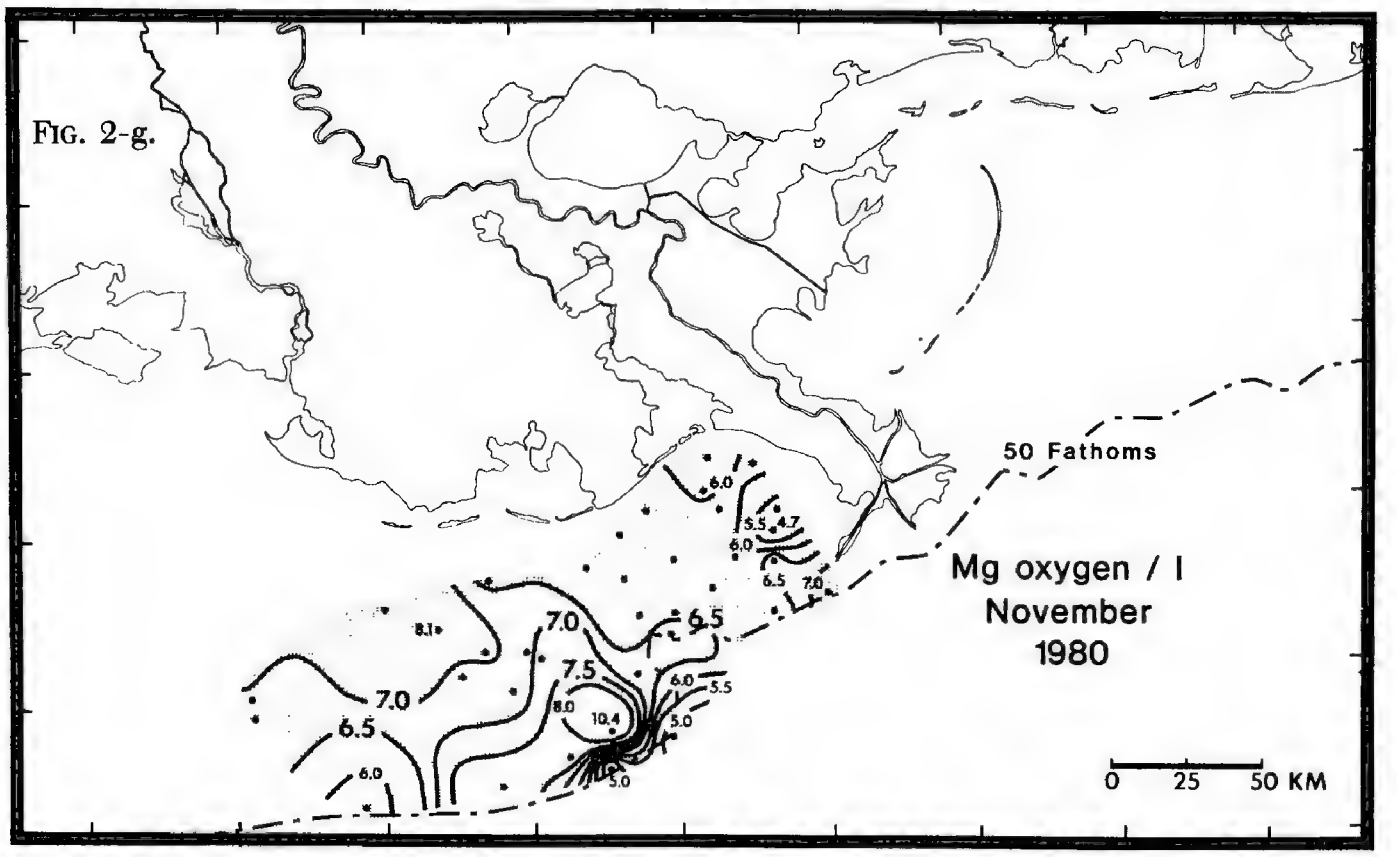
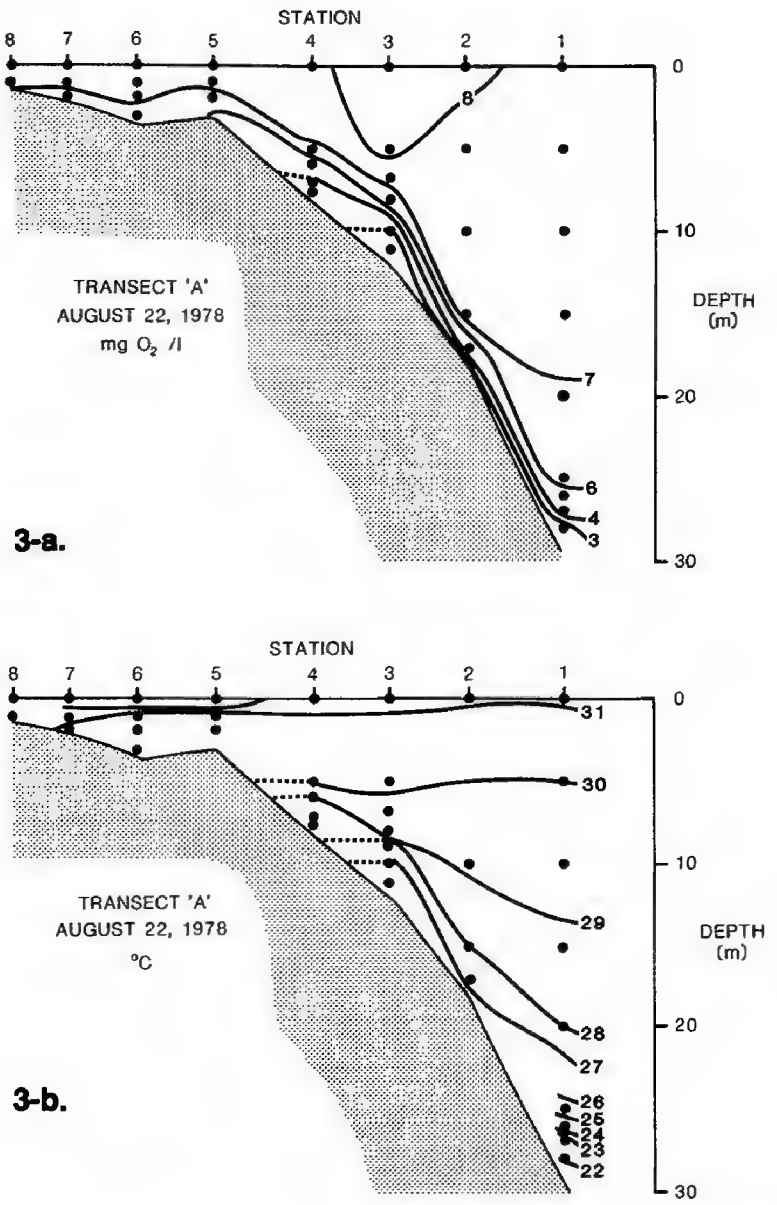



FIG. 2-g.

data from transect C (Fig. 3) seem to support this proposal, because oxygen values along this transect closely parallel the transmissometer readings that outline a bottom turbid layer. Transect A, east of the delta, also has a low-oxygen zone near the bottom. We did not measure light transmittance there. However, Griffin (1979) found a bottom turbid zone to be common west of the delta but to be absent east of the delta. Since hypoxic zones occur in both areas, oxidation of suspended sediments alone cannot therefore be invoked to explain differences in oxygen balances between the two areas.

Stratification is most severe during the summer (Wiseman *et al.*, this volume). The resulting isolation and reduced vertical mixing during calmer months may lead to oxygen depletion in the colder and saltier layer below. The approximate minimum respiration rates necessary to account for the average net 3 $mg \cdot l^{-1}$ loss between March and July, 1975 cruises would be 1 mg $O_2 \cdot m^{-3} \cdot hr^{-1}$ if no water exchange, reaeration, or photosynthesis occurred there. However, photosynthesis on the bottom may be significant. We have recovered apparently healthy sea grasses in bottom trawls from the eastern half of the study area and there are places on both sides of the delta where light on the bottom equals 3% of the surface value (Turner and Allen, unpublished data). Aside from photosynthetic and mixing processes, however, the respiration by either benthos or sinking plankton might possibly account for the 3 $mg \cdot l^{-1}$ oxygen concentration change from March to July. Benthic and water column respiration rates five times higher than that have been measured in areas with similar surface primary production and depth (Rowe *et al.* 1975; Hargrave 1973).

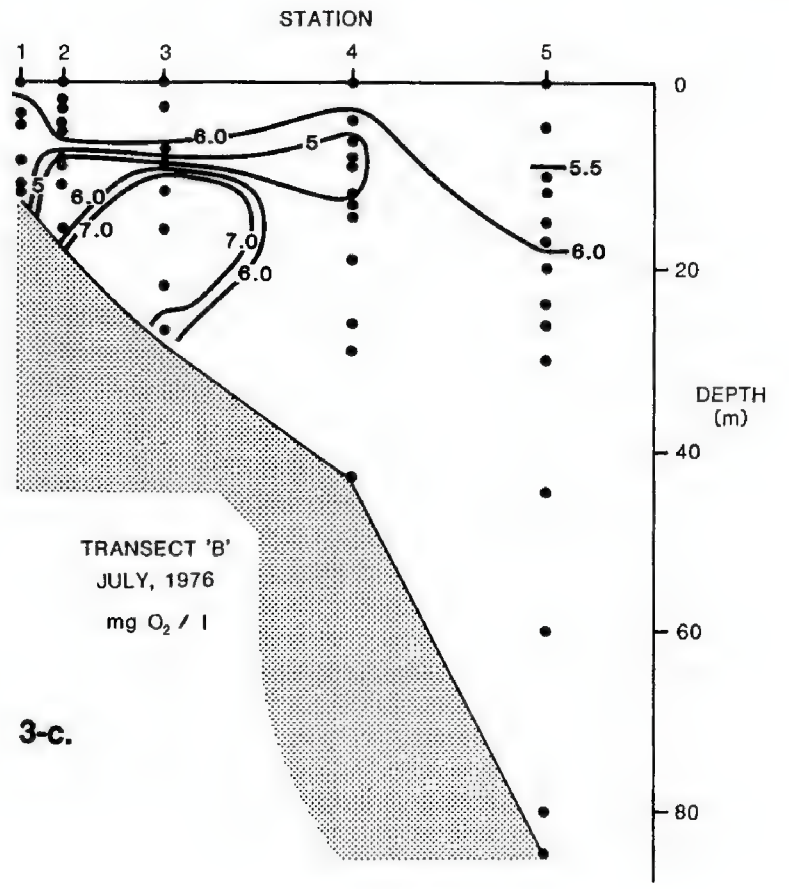
It is reasonable to expect regional benthic respiration rates to vary with regional variations in the respiration rates in the overlying water (Hargrave 1973). It is not known at present which has higher respiration rates, the



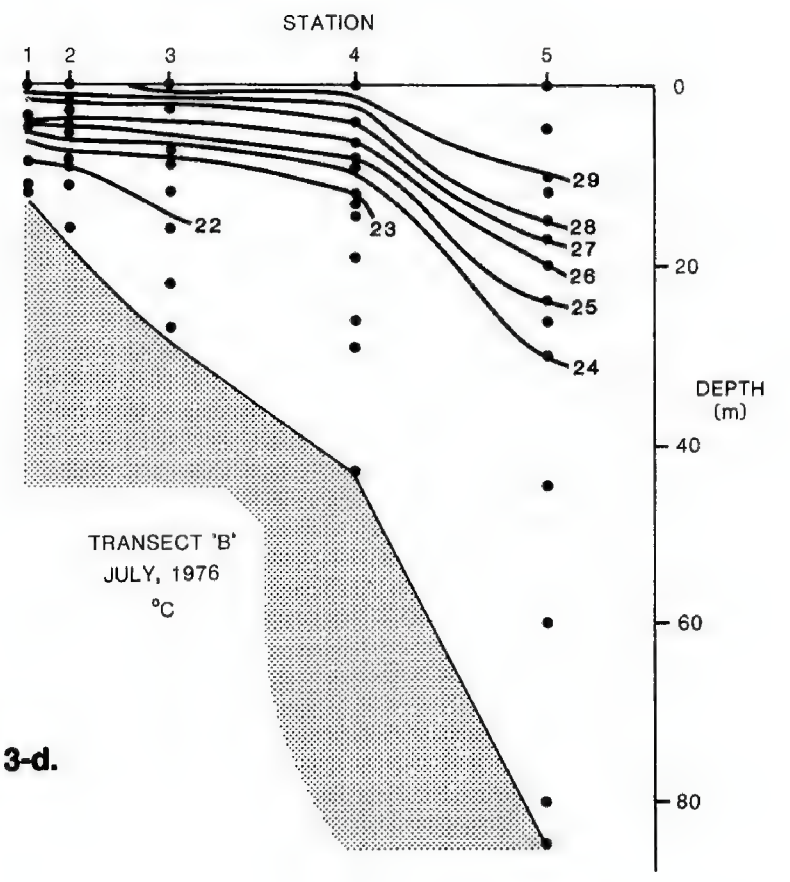

FIGS. 3 (a–g). Results from sampling in July 1976 and in August, 1978, along the three transects shown in Figure 2. Isopleths of oxygen (mg oxygen·$l^{-1}$), temperature (°C), and light transmittance (%) are shown.

pelagic or benthic community. Either could be very important in determining net oxygen balances. Equally important are the lack of vertical circulation, which thereby inhibits reaeration, *and* the absence of significant lateral mixing with more oxygenated water. Without rate measurements one cannot, however, determine the actual causal factors.

The relatively low oxygen concentrations found on the inner shelf west of the delta may be influenced by two other factors. Wiseman *et al.* (1982) have documented the transit of the Mississippi River plume into this area. Surface production is presumably entrained therein in a clockwise gyre whose nearshore terminus is directly over the area of 1 mg·$l^{-1}$ found in July 1975 (Fig. 3). The quantity of phytoplankton sinking at the terminus should be especially high there because phytoplankton production is much higher nearshore than it is in deeper waters, particularly at this site (Sklar and Turner 1981; Fucik and El-Sayed 1979). Secondly, Bayou LaFourche, laden with organic material, and serving as a sewage conduit for dozens of south Louisiana towns, empties directly north of the area where the lowest oxygen

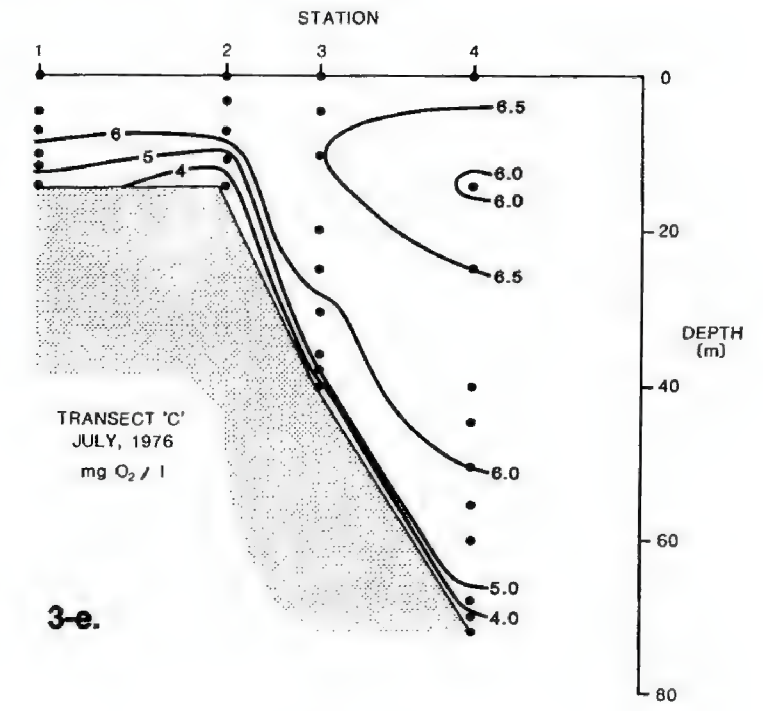



3-c.




3-d.

concentration was measured (0.4 $mg \cdot l^{-1}$; July 1975). Organic loading might be particularly high in this area. Measurements of oxygen consumption in the region would be desirable in determining the relative influence of these various factors.


STATION
1
2
3
4
0
20
40
60
80
DEPTH (m)
6
5
4
6.5
6.0
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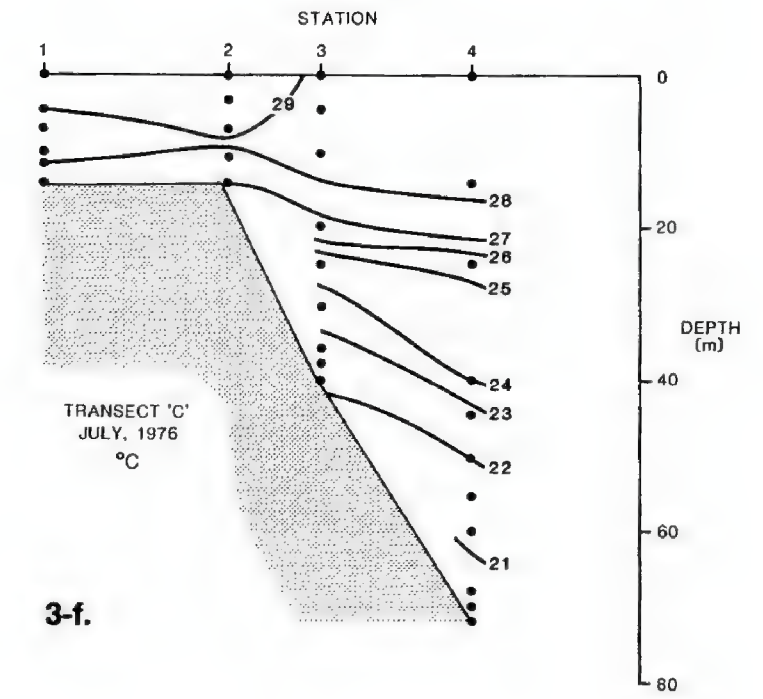
TRANSECT 'C'
JULY, 1976
mg $O_2$ / l

3-e.


STATION
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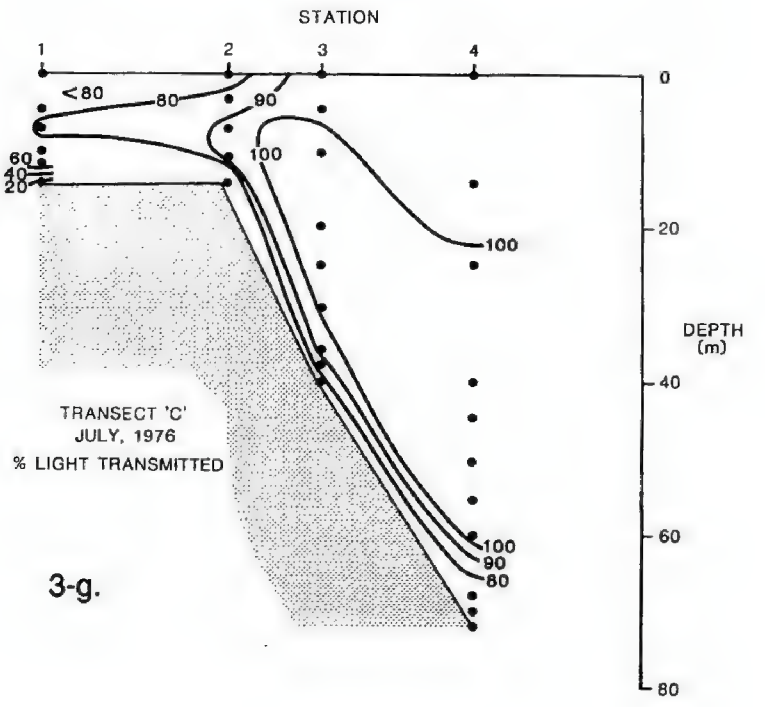
°C

3-f.


STATION
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TRANSECT 'C'
JULY, 1976
% LIGHT TRANSMITTED

3-g.

Finally, our measurements of oxygen concentration in bottom waters are generally higher than those of Ragan *et al.* (1978), even though our sampling periods overlapped in November 1975 and in January-February and July 1976. Their measurements of oxygen concentration in surface waters are greater than 110% saturation at 40% of their stations, and some values exceed 150% saturation. In November 1975, they estimated oxygen concentration of surface waters to be greater than 100% saturation in 31 of 37 stations west of the delta (along their transect D, E, and F). We can find no comparable values for these surface waters by authors who used oxygen titration, rather than the oxygen probe method (*e.g.*, Bull. Hydrographique 1932). Determination of the oxygen concentration in these surface waters is recommended in future research to check on the accuracy of previous measurements by means of oxygen probes and to understand the oxygen fluxes throughout the water column.

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## LITERATURE CITED

BEDINGER, C. A., J. W. COOPER, A. KWOK, R. E. CHILDERS and K. T. KIMBALL. 1981. Ecological investigations of petroleum production platforms in the central Gulf of Mexico. Volume 1, Part 1: Pollutant fate and effects studies. Final report submitted to the Bureau of Land Management for contract AA551-CT8-17. 149 pp.

BULLETIN HYDROGRAPHIQUE. 1932. Conseil Perm. Intl. L'Explor. Mer. Denmark (data report).

FOTHERINGHAM, N. and G. H. WEISSBERG. 1979. Some causes, consequences and potential environmental impacts of oxygen depletion in the northern Gulf of Mexico. Offshore Tech. Conf. Proc., **OTC 3611**:2205–2207.

FUCIK, K. W. and S. Z. EL-SAYED. 1979. Effect of oil production and drilling operations in the ecology of phytcplankton in the OEI study area. *Rice University Studies.* **65**(4&5):325–353.

GALLAWAY, B. J. 1981. An ecosystem analysis of oil and gas development in the Texas-Louisiana continental shelf. U.S. Fish and Wildlife, Biological Services Program. Publ. **FWS/OBS-81/27.** 9 pp.

GRIFFIN, G. M. 1979. Evaluation of the effects of oil production platforms on the turbidity of Louisiana shelf waters. *Rice University Studies.* **65**(4&5):159–179.

HARPER, D. E., JR., L. D. McKINNEY, R. R. SALZER and R. J. CASE. 1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. *Contributions in Marine Science.* **24**:53–79.

HARGRAVE, B. T. 1973. Coupling carbon flow through some pelagic and benthic communities. *Journal of Fisheries Research Board of Canada.* **30**:1317–1326.

MAY, E. B. 1973. Extensive oxygen depletion in Mobile Bay, Alabama. *Limnology and Oceanography.* **18**:353–366.

RAGAN, J. G., A. H. HARRIS and J. H. GREEN. 1978. Temperature, salinity and oxygen measurements of surface and bottom waters on the continental shelf off Louisiana during

portions of 1975 and 1976. *Professional Paper Series (Biology).* 3. Nicholls State Univ., Thibodeaux, LA. 29 p.

RICHARDS, F. A. and A. C. REDFIELD. 1954. A correlation between the oxygen content of sea water and the organic content of marine sediments. *Deep-Sea Research.* 1:279–281.

ROWE, G. T., C. H. CLIFFORD, K. L. SMITH, JR., and P. L. HAMILTON. 1975. Benthic nutrient regeneration and its coupling to primary productivity in coastal waters. *Nature, London.* 255:215–217.

SANTOS, S. L. and J. L. SIMON. 1980. Response of soft-bottom benthos to annual catastrophic disturbance in a south Florida estuary. *Marine Ecology—Progress Series.* 3:347–355.

SKLAR, F. H. and R. E. TURNER. 1981. Plankton production in the Louisiana coastal zone as influenced by the Mississippi River. *Contributions in Marine Science.* 24:93–106.

STRICKLAND, J. D. H. and PARSONS. 1968. A practical handbook of sea water analysis. *Bulletin, Fisheries Research Board of Canada.* 167. 309 pp.

WISEMAN, W. J., JR., S. P. MURRAY, J. M. BANE and M. W. TUBMAN. 1982. Physical environment of the Louisiana bight. *Contributions in Marine Science.* 25:109–120.

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# PLANKTON RESPIRATION RATES IN THE BOTTOM WATERS OF THE MISSISSIPPI RIVER DELTA BIGHT

R. E. Turner and R. L. Allen

*Coastal Ecology Laboratory, Center for Wetland Resources, Louisiana State University Baton Rouge, LA 70803-7507*

## ABSTRACT

Community plankton respiration (CPR) rates in the bottom waters of the Mississippi River Delta Bight ranged from 0.12 to 8 mg oxygen·$m^{-3}$·$h^{-1}$ in July and November, 1976. Mean values were similar on both cruises, and between east and west halves of the delta in July. The observed rates are high enough to influence significantly and possibly dominate factors influencing oxygen concentrations. The regional low oxygen concentrations that commonly occur are probably influenced as well by benthic respiration and by stratification. The role of suspended sediments in deriving variations in average CPR rates appears to be of minor importance since equal rates occurred in areas with and without a nepheloid layer. In July CPR was correlated with variations in chlorophyll *a* concentrations, thus indicating that phytoplankton sinking is probably a major factor determining regional variations in CPR.

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## INTRODUCTION

Oxygen concentration in the bottom waters of the Mississippi River Delta Bight is often 50% saturated over large areas, particularly in the summer (Turner and Allen 1982). These measurements are of ambient oxygen concentration and do not measure oxygen flux. They may reflect *in situ* respiration by the benthos or plankton, restricted re-aeration during pronounced stratification, on-welling of the oxygen-minimum layer from deeper waters in the Gulf of Mexico, or all of the above factors. For example, low oxygen conditions prevail as a result of plankton respiration below the photic zone in the Gulf of Panama (D'Croz *et al.* 1977) and in Puget Sound (Christensen and Packard 1976). Water column respiration is nearly as important as benthic respiration in the New York Bight (Garside and Malone 1978).

The purpose of the present investigation was to measure plankton community respiration rates in the bottom waters of the Mississippi River Delta Bight. We participated in two cruises, one in July during calm weather when the mean coastal currents were eastward, and another in November when currents flowed westward, and weather conditions were often stormy (Wiseman *et al.* 1982). Oxygen depletion times were computed from the plankton respiration rates in order to estimate the maximum impact of the observed rates on local oxygen balances.

## METHODS

We collected water samples with 2.5 liter Niskin bottles from within 3 m of the bottom on two cruises of the *R/V Oregon II*. Samples were not exposed to any bright light outdoors and to fewer than 25 $\mu E \cdot m^{-2} \cdot sec^{-1}$ in the laboratory. Subsamples were screened to remove organisms larger than 303 microns and concentrated 10 to 50 times in plastic filter-holding chambers of less than 20 ml volume. A presoaked cellulose 0.45-micron filter was in both upper and lower chambers. The filtrate from the higher experimental (respiration) chamber drained into the control chamber 4 cm below. Both chambers were without a stirring mechanism, and were equipped with sampling ports used to introduce sample water, to withdraw air bubbles, and to withdraw water after incubation. The filtrate was collected into the filter solely by gravity flow from a funnel placed 40 cm above the experimental chamber. Inlet and outlet ports were rubber tubes equipped with clamps. The chambers were constructed and treated as equals except that one held a concentrated plankton community. The total sample preparation from screening to incubation took less than 45 minutes. Both chambers were incubated in the dark at $\pm 2.0°C$ of *in situ* temperatures for 2 to 12 hours. Subsamples equal to no more than 40% of each chamber volume were subsequently carefully withdrawn from the chamber with a syringe and then introduced into a temperature-controlled micro-chamber that housed a silver-platinum oxygen electrode. The electrode was calibrated with the sodium-azide modification of the Winkler titration method (Strickland and Parsons 1968). Differences in the oxygen concentration between control and experimental chambers were noted by repeated comparison of injections from the two syringes. An expanded scale recorder was also useful to detect the smaller differences. No difference in oxygen concentration between experimental and control chambers was ever detected at time = zero. The differences between chambers after incubation was, therefore, attributed to respiration during incubation. The accuracy of electrode calibration was certainly within 0.1 mg/1. Single, rather than replicate, samples were taken in order to increase the sampling area. The coefficient of variation for four samples was typically 20%. Respiration rates as low as 0.1 $mg \cdot m^{-3} \cdot h^{-1}$ can be detected with this method.

We determined bottom water oxygen concentrations in the fresh samples by using the Winkler method and phaco-pigment free chlorophyll *a* using a spectrophotometer (Strickland and Parsons 1968). The time that the *in situ* oxygen concentration would take to be depleted to zero at the observed respiration rates was calculated and termed the oxygen depletion time (days). Such calculations ignore the effects of lateral mixing and benthic respiration on oxygen deficits and are used here to understand the impact of the plankton community alone on the oxygen concentration.

## RESULTS

The mean plankton respiration (CPR) rates in the bottom waters for all 61 samples ranged from 0.1 to 8 mg $O_2 \cdot m^{-3} \cdot h^{-1}$. In July and November the average CPR rate ($\pm 1$ std. dev.; number = n) for the west delta was 2.2 ($\pm 2.2$; n = 31) and 2.8 ($\pm 2.3$; n = 30) mg $O_2 \cdot m^{-3} \cdot h^{-1}$, respectively. The average CPR rates ($\pm 1$ std. dev.) were 2.16 ($\pm 2.27$; n = 18) and 2.20 ($\pm 2.16$; n = 13) mg $O_2 \cdot m^{-3} \cdot h^{-1}$, for east and west deltas, respectively, in July. The mean rates were thus nearly equal and the standard deviation large so that a student's *t* test for differences between either the average rates for the whole shelf on different cruises or between east and west sides of the delta in July did not support the hypothesis of statistically significant differences at the 5% level.

The geographic distribution of CPR is shown in Figures 1 and 2 together with the oxygen depletion times. It is worthwhile to note the absence of the highest CPR rates at stations nearest the delta on both cruises. The oxygen

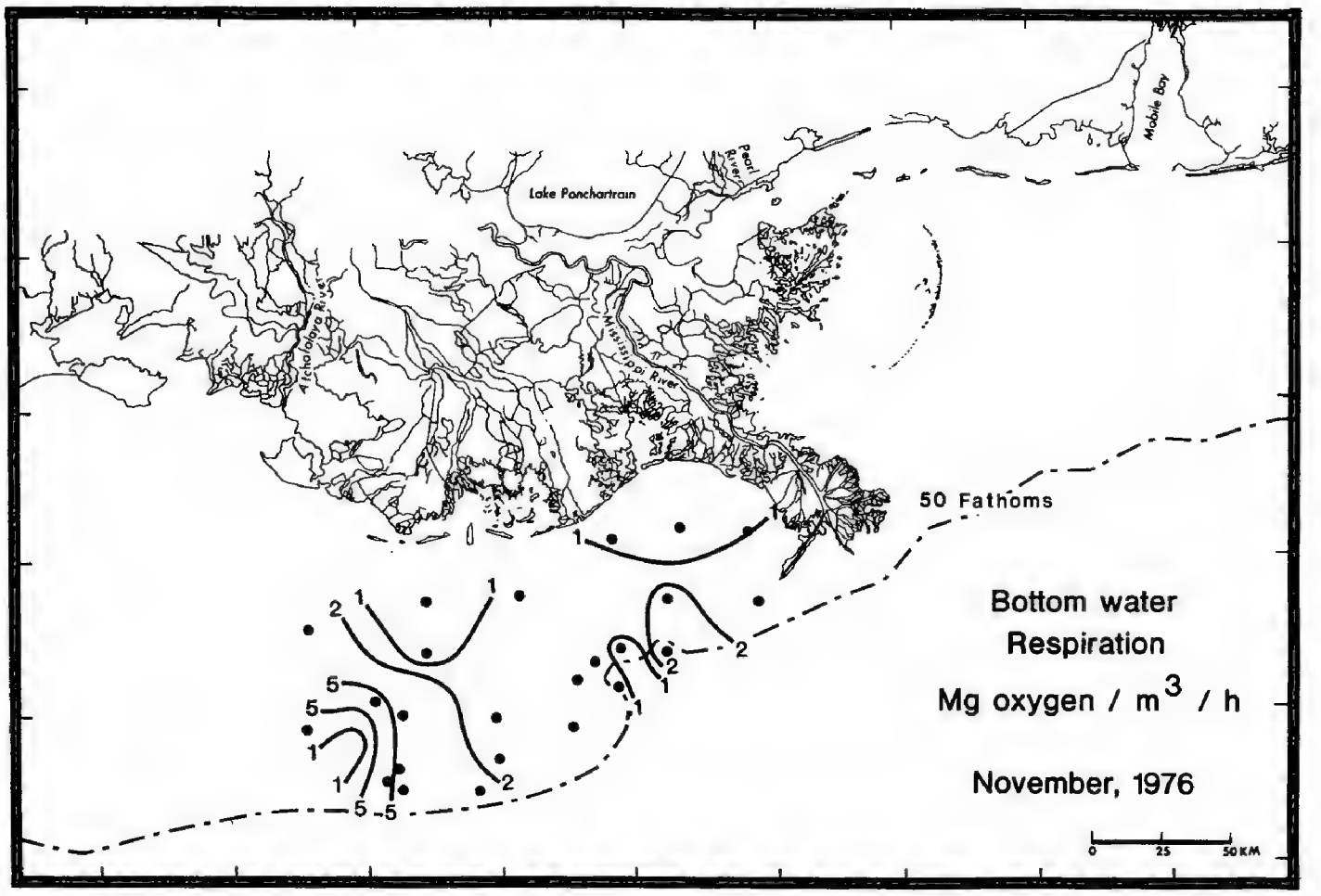


FIG. 1. Community plankton respiration rates of bottom waters November 1976 (top) and the days necessary to deplete the observed oxygen concentration to zero at the measured CPR (bottom). Some sites have duplicate sampling.

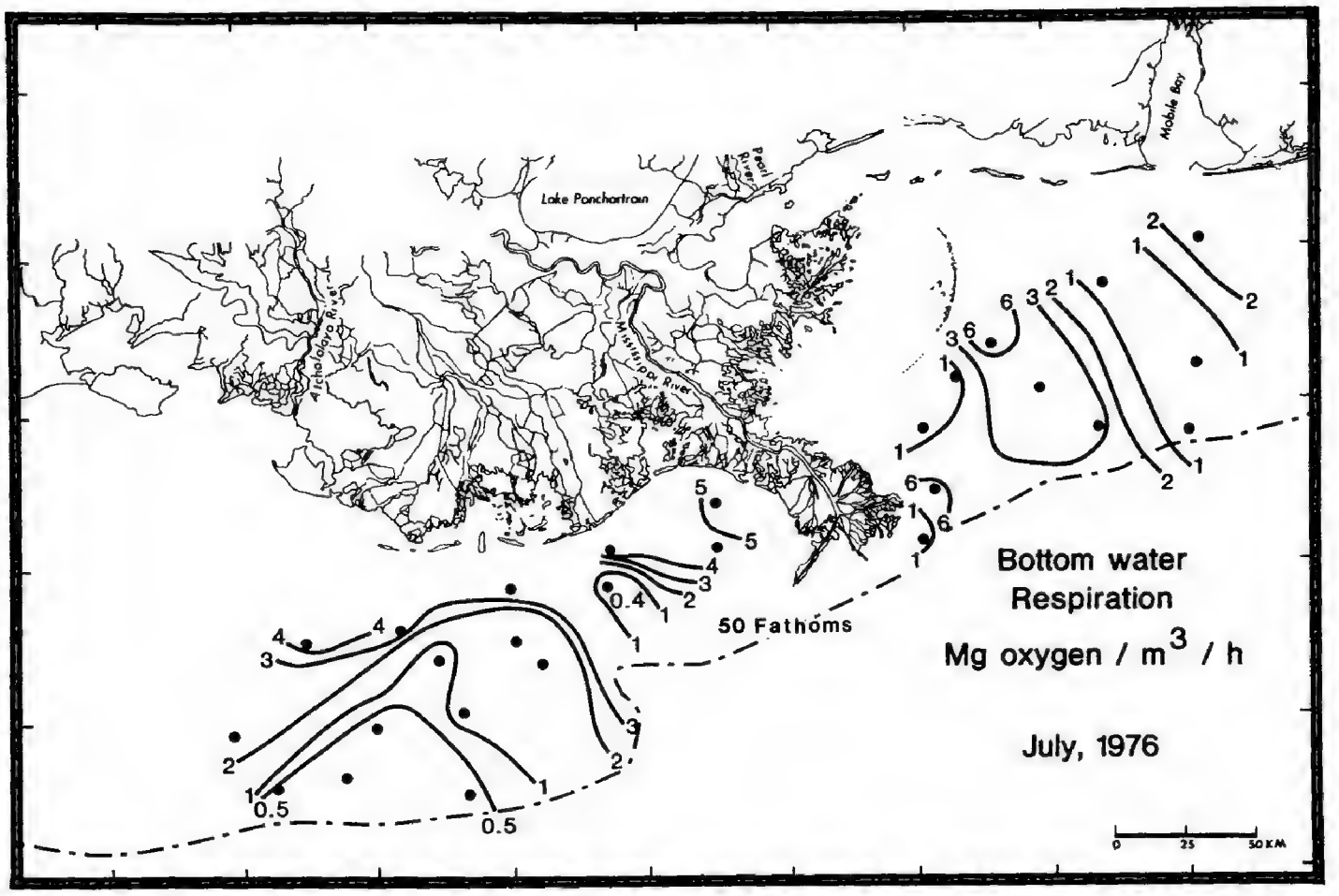


FIG. 2. Community plankton respiration rates of bottom waters in July 1976 (top) and the days necessary to deplete the observed oxygen concentration to zero at the measured CPR (bottom). Some sites have duplicate sampling.

depletion rates were between two and thirty months. The geographic distribution of CPR generally indicates that areas with the shortest oxygen depletion time had the highest CPR rates. However, oxygen concentration values are not uniform across the shelf, so that areas with nearly equal CPR rates may have different depletion times.

Chlorophyll *a* concentrations are available for only 15 samples when respiration rates were made (Fig. 3). There is a statistically significant relationship between pigments and CPR for the November cruise ($\alpha = 0.05$). The coefficient of determination ($R^2$) equaled 0.30.

## DISCUSSION

The observed CPR is about what is to be expected for waters this productive. Primary production rates of 200 to 300 g C $m^{-2} \cdot y^{-1}$ have been

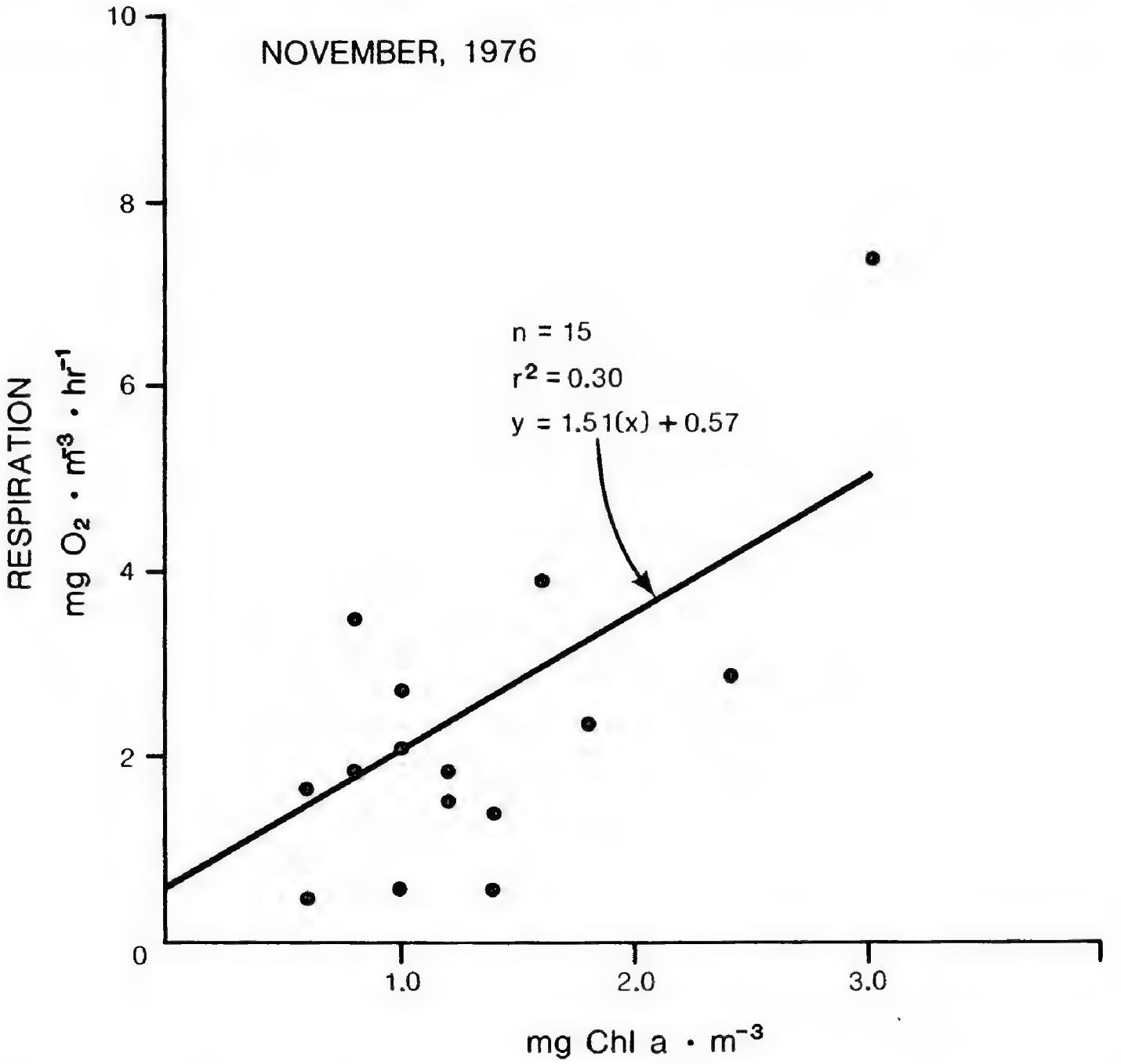


FIG. 3. Community plankton respiration rates of bottom waters in November 1976 as related to chlorophyll *a* concentrations.

estimated for two areas west of the delta (Fucik and El-Sayed 1979, Sklar and Turner 1981). CPR rates, measured with a different technique, are in the same range off the coast of Georgia where primary production rates are similar (Turner manuscript). CPR rates are directly related to chlorophyll concentrations in the Gulf of Maine (Packard and Williams 1981), the Peru upwelling (Setchell and Packard 1979), and off the Georgia coast (Turner manuscript). Fucik and El-Sayed (1979) and Sklar and Turner (1981) report that chlorophyll *a* concentrations at the bottom of the euphotic zone may be equal or greater than at the surface. The ratio of CPR:chlorophyll *a* may vary somewhat between methods employed to measure CPR. However, the 1–2 mg Chl $a \cdot l^{-1}$ measured below the euphotic zone in the Mississippi River Bight is high enough to explain the observed CPR rates and there is a significant correlation at the 95% level between the two variables (Fig. 3). Packard and Williams (1981) provide data on both CPR and chlorophyll *a* within the euphotic zone of the Gulf of Maine. There is a strong linear relationship between the two variables there, but the ratio of CPR:Chl *a* in their study is four times that found in this study. They employed a direct Winkler titration of samples collected in bottles incubated for 11 to 24 hours. Whether the differences between the results reported here and in their study is the result of diel, light adaptation, physiological or methodological variations, remains to be investigated. But the implication is that phytoplankton sinking from the very productive surface waters is the source of organic substrates being respired. This conclusion is supported by an analysis of the distribution of CPR rates around the delta. If riverine sediments were the major source of organic materials, then the rates should be highest near the delta where they settle out, lowest east of the delta where the nepheloid layer is absent, and highest on the western side where the nepheloid layer is present (Griffin 1979). Neither a deltaic concentration of CPR nor an east-west difference is observed. Furthermore, phytoplankton sinking from surface to benthos is a well-established driving force of variations in benthic respiration rates (*e.g.*, Hargrave 1973; Garside and Malone 1978; Bienfang 1980).

Although CPR rates were nearly equal in July and November, the oxygen concentrations were lowest during the summer (Turner and Allen 1982). Other oxygen sinks, or less mixing and re-aeration, may also be involved as causal factors. Stratification is certainly more severe in summer (Wiseman *et al.* 1982), but we cannot yet effectively evaluate its impact on re-aeration and mixing coefficients. Also, the benthic respiration per square m in other marine environments of equivalent surface production (*e.g.*, Rowe *et al.* 1975) may equal or exceed the CPR rate in one cubic m of bottom water off the Louisiana coast. In the four months after a March, 1975, cruise, the oxygen concentration in bottom waters decreased about 3 $mg \cdot l^{-1}$ (Turner and Allen 1982). A CPR rate of 1.0 $mg \cdot m^{-3} \cdot h^{-1}$ would have been necessary to remove this much oxygen if benthic uptake, reaeration, and mixing are presumed negligible. We have routinely measured twice this rate in most samples. Under the right conditions of reduced mixing CPR rates alone may

thus be sufficient to result in the observed low oxygen zones. We suspect that benthic respiration rates may also be significant in this regard and will report on that aspect elsewhere.

## ACKNOWLEDGEMENTS

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## LITERATURE CITED

BIENFANG, P. K. 1980. Phytoplankton sinking rates in oligotrophic waters off Hawaii, U.S.A. *Marine Biology.* **61**:69–77.

CHRISTENSEN, J. P. and T. T. PACKARD. 1976. Oxygen utilization and plankton metabolism in a Washington fjord. *Estuarine and Coastal Marine Science.* **4**:339–347.

D'CROZ, L. D., B. KWIECINSKI and V. MARTINES. 1977. Un caso de mortandad natural de peces en la Bahia de Panama. pp. 683–694. Actas del IV Simposium Internacional de Ecologica Tropical. Smithonian Tropical Research Institute, Panama, Panama. 1038 pp.

FUCIK, K. W. and S. Z. EL-SAYED. 1979. Effect of oil production and drilling operations in the ecology of phytoplankton in the OEI study area. *Rice University Studies.* **65**(4&5):325–353.

GARSIDE, C. and T. C. MALONE. 1978. Monthly oxygen and carbon budgets of the New York Bight apex. *Estuarine and Coastal Marine Science.* **6**:93–104.

GRIFFIN, G. M. 1979. Evaluation of the effects of oil production platforms on the turbidity of Louisiana shelf waters. *Rice University Studies.* **65**(4&5):159–179.

HARGRAVE, B. T. 1973. Coupling carbon flow through some pelagic and benthic communities. *Journal of the Fisheries Research Board of Canada.* **30**:1317–1326.

PACKARD, T. T. and P. J.LEB. WILLIAMS. 1981. Rates of respiratory oxygen consumption and electron transport in surface seawater from the northwest Atlantic. *Oceanologica Acta.* **4**(3):351–358.

ROWE, G. T., C. H. CLIFFORD, K. L. SMITH, JR. and P. L. HAMILTON. 1975. Benthic nutrient regeneration and its coupling to primary productivity in coastal waters. *Nature, London.* **255**:215–217.

SETCHELL, F. W. and T. T. PACKARD. 1979. Phytoplankton respiration in the Peru Upwelling. *Journal of Plankton Research.* **1**:343–354.

SKLAR, F H. and R. E. TURNER. 1981. Plankton production in the Louisiana coastal zone as influenced by the Mississippi River. *Contributions in Marine Science.* **23**:93–106.

STRICKLAND, J. D. H. and PARSONS. 1968. A practical handbook of sea water analysis. *Bulletin, Fisheries Research Board of Canada.* **167.** 309 pp.

TURNER, R. E. and R. L. ALLEN. 1982. Oxygen concentrations in the bottom waters of the Mississippi River delta bight. *Contributions in Marine Science.* **25**:161–172.

WISEMAN, W. J., JR., S. P. MURRAY, J. M. BANE and M. W. TUBMAN. 1982. Physical environment of the Louisiana Bight. *Contributions in Marine Science.* **25**:109–120.

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# INFLUENCE OF THE MISSISSIPPI RIVER ON THE SPATIAL DISTRIBUTION OF MICROHETEROTROPHIC ACTIVITY IN THE GULF OF MEXICO

Roger B. Hanson

*Skidaway Institute of Oceanography, Post Office Box 13687, Savannah, Georgia 31406*

## ABSTRACT

Spatial distribution of microheterotrophic activity in the water column of the Mississippi Delta Bight and the Gulf of Mexico was investigated in April and May 1977. Microheterotrophic activity was determined from the uptake of labeled [$^{14}$C] glucose and the concentration of reactive carbohydrates. Mississippi River water was characterized by particulate organic carbon (POC) concentration and hydrographic data.

Microheterotrophic activity decreased with distance offshore and with increasing depth of the water column in the Mississippi Delta Bight. Highest activity was in waters with low salinities and high POC concentrations. Where the salinities were characteristic of open Gulf of Mexico waters, microheterotrophic activities were typically low. Waters with warmest temperatures did not always possess the highest microheterotrophic activity. In surface waters of the Gulf of Mexico, activity was lower than in the Bight and activity decreased with increasing depth. Turnover times of carbohydrates were inversely proportional to the rate of microheterotrophic activity. Reactive carbohydrates did not show any gradients with either distance from shore or depth of the water column. Respiration ([$^{14}$C] $CO_2$) of the labeled glucose was highest in surface waters and decreased with distance from shore. The results suggest that the Mississippi River greatly influences the spatial distribution of microheterotrophic activity in the Mississippi Delta Bight but not in the Gulf of Mexico.

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## INTRODUCTION

Microheterotrophic activities in marine environments are frequently related to nutrient, suspended solid, and particulate organic carbon concentrations (Fuhrman *et al.* 1980, Hanson and Snyder 1980, Bent and Goulder 1981, Hanson *et al.* 1982a). Because dissolved and particulate organic carbon is delivered to coastal waters by terrestrial runoff, rivers are major sources of allochthonous materials to the ocean (Goldberg 1971, Gravine 1974, Gravine and Monk 1974). Autochthonous production of organic matter in the ocean occurs most notably when inorganic nutrients are upwelled near continental shelves or at equatorial divergences (Wangersky 1977).

The Mississippi Delta Bight (Fig. 1) receives freshwater and nutrients

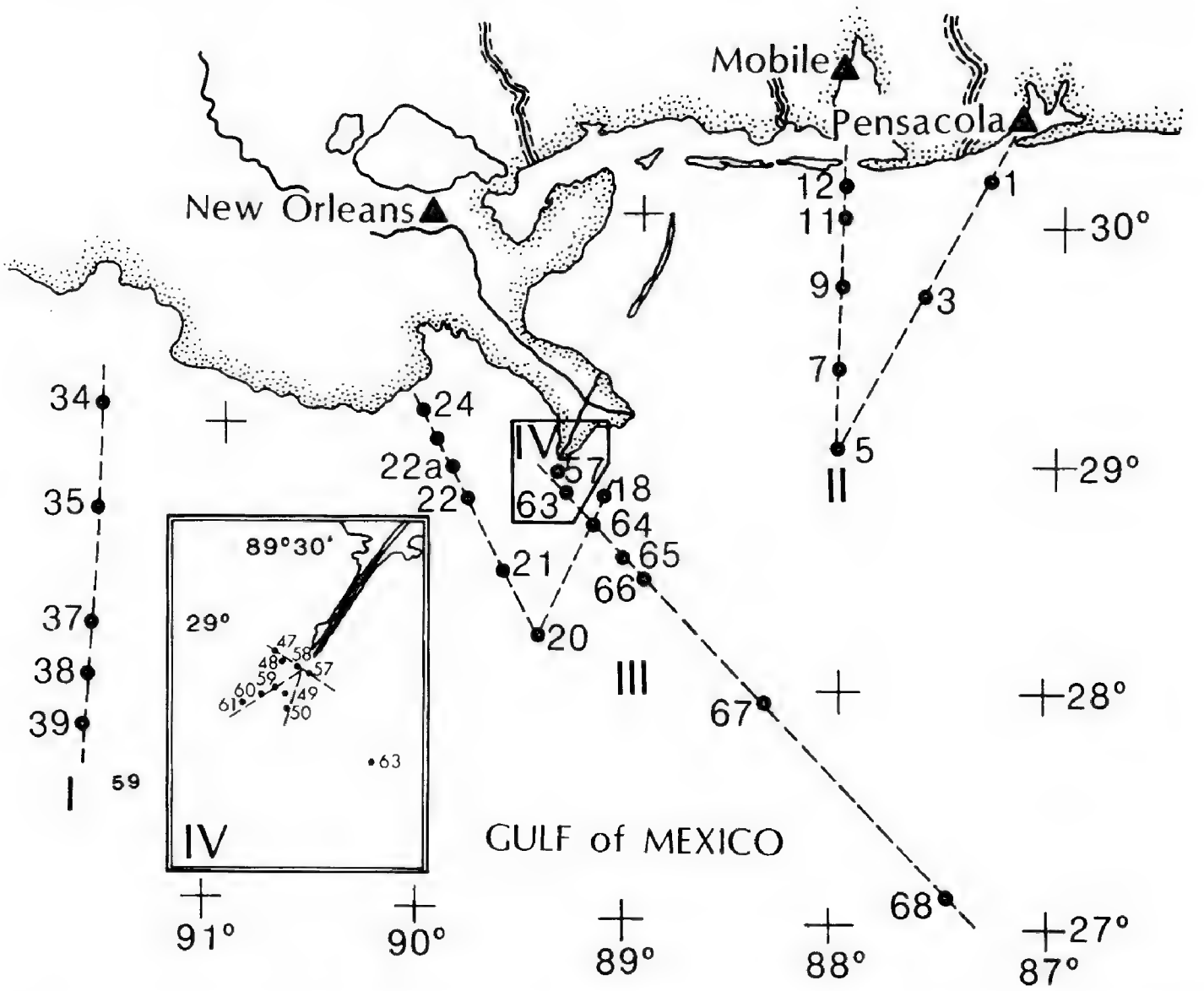


FIG. 1. Location of hydrographic stations in the Mississippi Delta Bight which were sampled for microheterotrophic activity between 27 April and 9 May 1977. Zone I, II, III and IV were arbitrarily designated to represent different areas in the Bight.

from one of the world's longest rivers, the Mississippi River. Water flow through the Delta bifurcates along several channels before entering the Gulf of Mexico. The southwest channel delivers the largest volume of water to the Gulf. Historically, the effects of hydrocarbon pollution from offshore oil platforms and other pollutants from the Mississippi River have been studied in this area of the Gulf coast off Louisiana and Mississippi (Ojuesky *et al.* 1979, Alexander and Schwarz 1980). The influence of the Mississippi River on microheterotrophic activities in the Bight has not been previously studied.

This report describes the spatial distribution of microheterotrophic activities in relation to particulate organic carbon and hydrographic features. Several cross-sections of the Bight were made to study the frontal structures of the River's plume and the influence of the River on microheterotrophic activities in the Gulf of Mexico.

## METHODS

Hydrographic data were collected during the R/V EASTWARD cruise (E-1-J-77) off the coasts of Louisiana, Mississippi, Alabama and Florida between 27 April and 9 May, 1977 (Fig. 1). Salinity and temperature were determined at stations with water depths of less than 100 m (Allen and Turner 1977) by means of STD (Plessy Environmental Systems) and surface-bucket thermometers. Temperatures and salinities were obtained at each depth sampled for microheterotrophic activity. Cross-sectional plots were used to illustrate the physical features of the water column and the River's influence on microheterotrophic activity.

### Measurement of Microheterotrophic Activity

**Uptake of [$^{14}$C] Glucose.** Water was collected in 10 l Niskin bottles, previously rinsed with 70% alcohol. Subsamples (50 or 100 ml) were dispensed into baked (450°C for 4 hours) serum bottles (250 ml volume). Three replicate bottles received uniformly labeled [$^{14}$C] glucose (Amersham Searle Co.) to yield a final concentration of 3 μg glucose/l and were then incubated at ambient water temperature (± 1°C). In coastal and shelf waters (< 100 m), samples were incubated for about 2 hours. Samples from the Gulf of Mexico (> 100 m) were incubated for 6 hours. For a zero-time control, one replicate was poisoned with 2 N $H_2SO_4$-5% formaldehyde before labeled glucose was added. At the end of the incubation, 2 or 4 ml of acid-formaldehyde solution was added to the sample. The effect of acid-formaldehyde fixation on the recovery of assimilated [$^{14}$C] glucose can be great (Griffiths *et al.* 1975; Hanson and Wiebe 1977). For this reason, the presumed assimilation fraction is a conservative estimate of actual amount taken up and not respired. Respired [$^{14}$C]$CO_2$ was trapped on Whatman No. 1 paper wicks saturated with 0.25 or 0.5 ml of phenylethylamine (Hobbie and Crawford 1969), by periodic mixing of samples for 24 hours at laboratory temperature (~ 25°C). The wicks were then removed and placed in mini scintillation vials. A standard (PPO/POPOP/toluene) scintillation fluor (5 ml) was added and the samples were stored at −5°C. The water was filtered through 0.45 μm (47 mm diameter) Millipore®, HA filters, and the filters rinsed twice with 10 ml of filtered seawater. Filters, dried at 50°C for 24 hours, were cleared with 15 ml of scintillation fluor and counted for 20 minutes or 20,000 counts. Internal standards were added to replicate samples from Zones I, II, III, and IV (Fig. 1) and a quench factor was used to convert counts to disintegrations/minute.

**Glucose Measurements.** Glucose concentrations were estimated by an enzymatic-fluorescent technique (Hicks and Carey 1968). However, recently we found that this procedure also detects other reactive carbohydrates in the free, dissolved carbohydrate pool (Hanson and Snyder 1979a). In general, glucose comprises more than 60% of the free, dissolved carbohydrates in seawater (Mopper *et al.* 1980, Ittekot *et al.* 1981). Therefore, reactive carbohydrates are expressed in terms of glucose equivalents. The sensitivity of assay for analytical grade glucose was ±2 μg/l. On board ship, water samples (30 ml) were filtered through baked (450°C for 4 hours) Gelman-GF/C filters at a vacuum of 5 cm of Hg. Samples were stored in plastic vials under dry ice at −20°C until analysis.

**Calculation of Microheterotrophic Activity.** Because other reactive carbohydrates are included with the glucose assay (see Discussion), the actual rate of glucose uptake by the microheterotrophs could not be determined. The amount of labeled glucose (3μg/l) added to samples was always an order of magnitude or more lower than the concentrations of reactive carbohydrates (see Table 1). In theory, the uptake of labeled glucose was a tracer experiment. Therefore, the rates that were measured provide an assessment of microheterotrophic activity. Microheterotrophic activity (μg glucose/l·h) was calculated in terms of [$^{14}$C] glucose uptake (assimilation plus respiration) and the reactive carbohydrate (glucose) concentration (Wright and Hobbie 1965, Vaccaro and Jannasch 1966). The actual flux in these waters is no doubt lower than the rates calculated. However, the rates provide a conservative estimate of the carbohydrate flux.

**Particulate Organic Carbon Measurement.** On board ship, 50 ml (Zone IV) and 500 to 1000 ml (Zones I, II and III) of water were filtered through Gelman GF/C filters. The filters were prepared for wet oxidation using procedures described in Strickland and Parsons (1972). The method may give higher estimates of POC than direct combustion methods but are within 10 to 20% of the carbon content of particulate material.

## RESULTS

### Microheterotrophic Activity

Microheterotrophic uptake of the labeled glucose was investigated over time with a nearshore and an offshore population (Fig. 2). Uptake by the

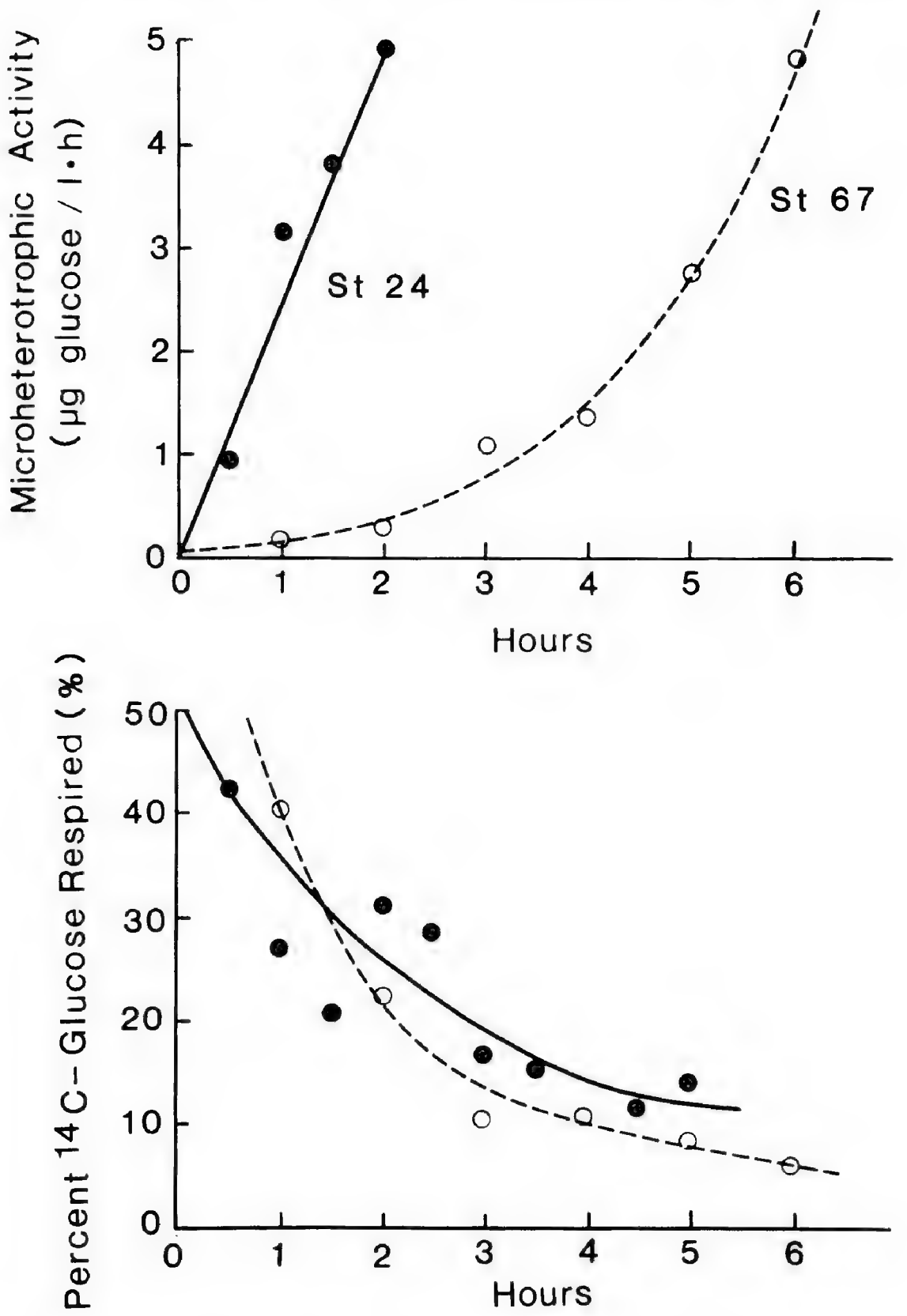


FIG. 2. Microheterotrophic response to added $^{14}$C-glucose (3 µg/l): uptake of labeled glucose with time (A) and percentage of labeled glucose respired with time (B) for nearshore (•) and offshore (o) populations in the Mississippi Delta Bight.

nearshore population was linear for five hours (data not shown for the period three to five hours) whereas uptake by the offshore population increased exponentially. The initial rates (0–2 hrs) for the offshore population were an order of magnitude lower than the nearshore population. The percentage of [$^{14}$C] glucose respired by the two populations was similar over time but decreased exponentially with incubation time.

## Cross-Section Variability

**Zone I.** Microheterotrophic activity was highest near the bottom on the western shelf of the Mississippi Delta (Fig. 3). The activity and percent respired decreased with distance from shore and with depth of the water column. Turnover times of the reactive carbohydrate pool showed similar isopleths as microheterotrophic activity. Shortest turnover times of 4 hours occurred near the bottom at Station 34 while turnover times for most of the shelf waters were between 5 and 10 hours. Longest turnover times of 6,760 hours were in deep water at Station 39. POC concentrations were highest (110–175 μg C/l) near the shelf bottom and lowest at the surface.

Temperature and salinity profiles along this transect indicated little structure in the water column (Fig. 9). Temperatures were between 22 and 23°C over most of the shelf while salinity varied from 20‰ in surface-shelf water to 36‰ in the Gulf of Mexico.

The concentrations of reactive carbohydrates (as glucose) in the Bight and Gulf of Mexico ranged between 30 and 100 μg/l. No trend was observed with distance from shore or with depth. For comparison, concentrations in Zone I and III—Gulf of Mexico are given in Table 1.

**Zone II.** Microheterotrophic activity on the western side of the Mississippi Delta was similar to Zone I (Fig. 4). Highest activity occurred in the surface waters near shore (Station 12) and decreased with distance from shore and with depth of the water column. Shortest turnover times were found off Mobile Bay. The highest percentage of respired [$^{14}$C] glucose was measured off Pensacola Bay. Most respiration values in Zone II were between 10–20%. Particulate organic carbon concentrations were between 100 and 170 μg/l over this area of the shelf.

The spatial distribution of microheterotrophic activity and turnover times in Zone II coincided with temperature and salinity (Fig. 9). Highest activity and shortest turnover times were in waters with temperatures of 22°C and salinity of 25‰. These waters also had some of the highest concentrations of POC. Waters with temperatures of 23°C and salinities of 35 to 36‰ possessed the lowest activity and longest turnover times.

**Zone III—Delta.** Highest variability in activity and respiration was found in an area near the southwest and south entrances to the Mississippi River (Fig. 5). Highest microheterotrophic activity and percent respired, and shortest turnover times were found near Grand Isle. Although values generally decreased (turnover times increased) with depth in the water column, values from surface waters did not decrease with distance offshore as in Zones I and II. Respiration had least variability in surface waters,

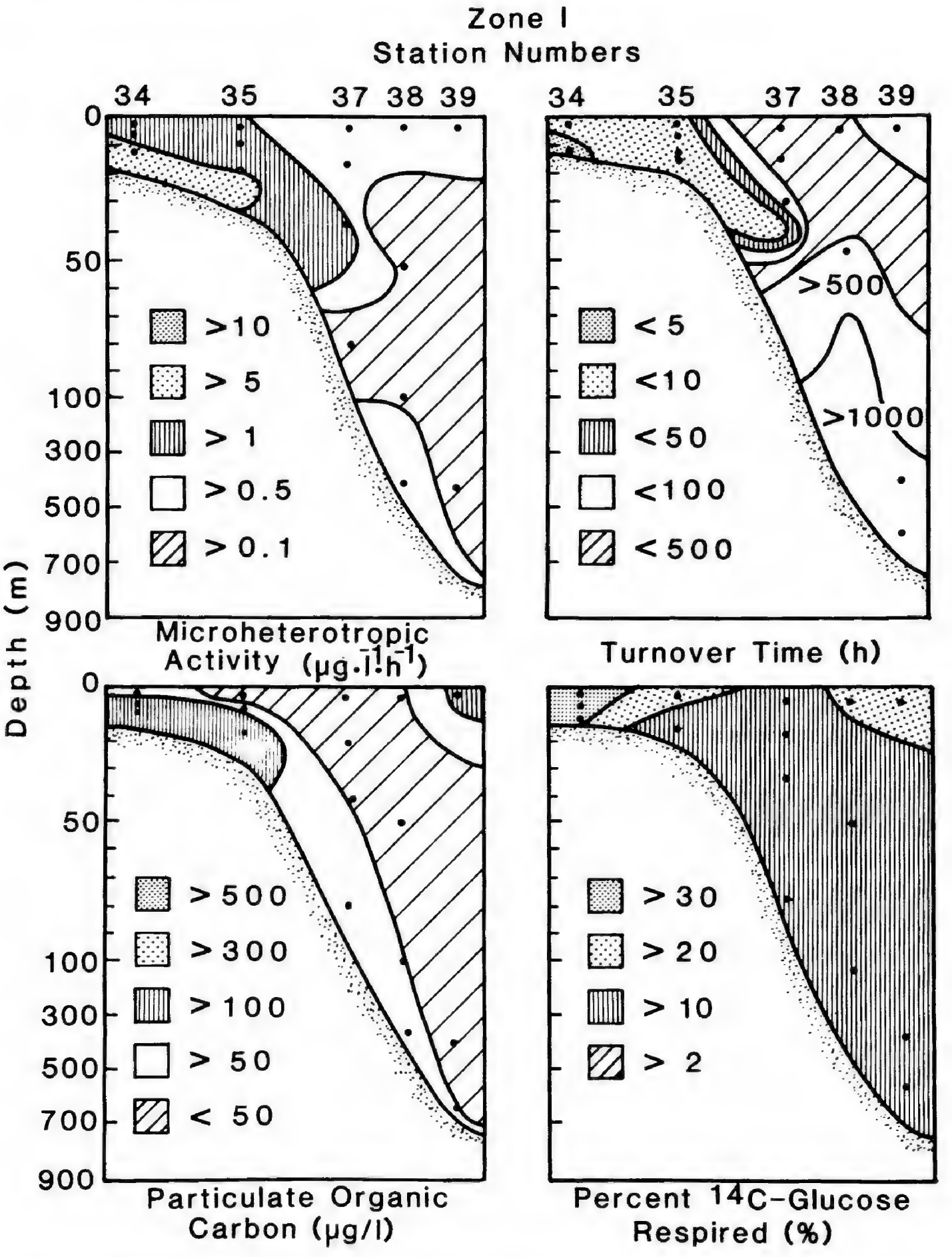


FIG. 3. Microheterotrophic activity, turnover time for the measured glucose, percentage of labeled glucose respired and particulate organic carbon concentrations in Zone I of the Mississippi Delta Bight.

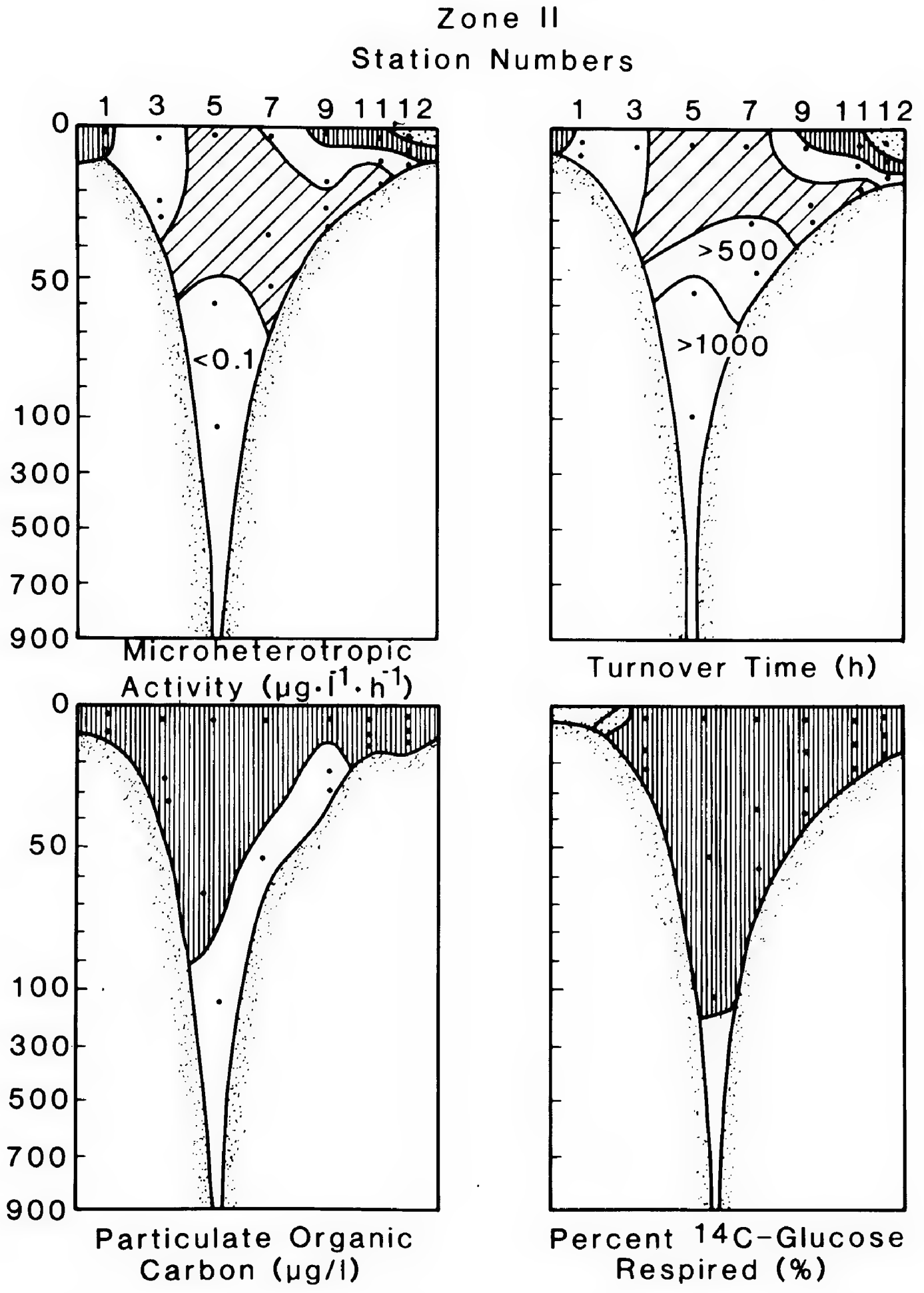


FIG. 4. Microheterotrophic activity, turnover time for the measured glucose, percentage of labeled glucose respired and particulate organic carbon concentrations in Zone II of the Mississippi Delta Bight.

TABLE 1

**Concentrations of reactive carbohydrates (expressed in glucose units) in waters of the Mississippi Delta Bight and the Gulf of Mexico.**

| ZONE III-GULF OF MEXICO | | | ZONE I | | |
|---|---|---|---|---|---|
| Stations | Depth (m) | Concentrations (µg/l) | Stations | Depth (m) | Concentrations (µg/l) |
| 57 | 0 | 98 | 34 | 3 | 77 |
| | 3 | 55 | | 5 | 33 |
| | 10 | 36 | | 8 | 36 |
| 63 | 3 | 70 | 35 | 3 | 39 |
| | 20 | 55 | | 8 | 74 |
| | 60 | 54 | | 15 | 42 |
| | 95 | 50 | | | |
| 64 | 3 | 57 | 37 | 3 | 39 |
| | 40 | 40 | | 20 | 46 |
| | 120 | 57 | | 40 | 37 |
| | 205 | 58 | | 80 | 47 |
| 65 | 0 | 93 | 38 | 3 | 70 |
| | 50 | 41 | | 50 | 67 |
| | 150 | 54 | | 100 | 30 |
| | 250 | 48 | | 390 | 43 |
| | 350 | 49 | | | |
| 66 | 3 | 54 | 39 | 3 | 36 |
| | 200 | 67 | | 200 | 48 |
| | 400 | 38 | | 400 | 66 |
| | 600 | 38 | | 650 | 68 |
| 68 | 3 | 60 | | | |
| | 50 | 71 | | | |
| | 100 | 55 | | | |
| | 300 | 40 | | | |
| 69 | 3 | 50 | | | |
| | 50 | 44 | | | |
| | 100 | 53 | | | |
| | 300 | 35 | | | |

although some low values (10–20%) were found at the surface at Stations 22 and 22A. Low percentages of respired glucose (2–10) in waters below the 10 to 20% isopleth were not noted in Zone I and II. Highest POC concentrations (685 to 695 µg/l) were found in surface waters of Stations 18 and 24.

Hydrographic data also showed variability along these transects (Fig. 9). Most high values for POC and microheterotrophic activity were in waters with temperatures of 23°C and salinities between 20 and 30‰. Lowest activities were found at Stations 20 and 22A where salinities were between 30 and 36‰.

**Zone III—Gulf of Mexico.** A cross-section from the Mississippi Delta into the Gulf of Mexico showed gradients with distance offshore and depth (Fig.

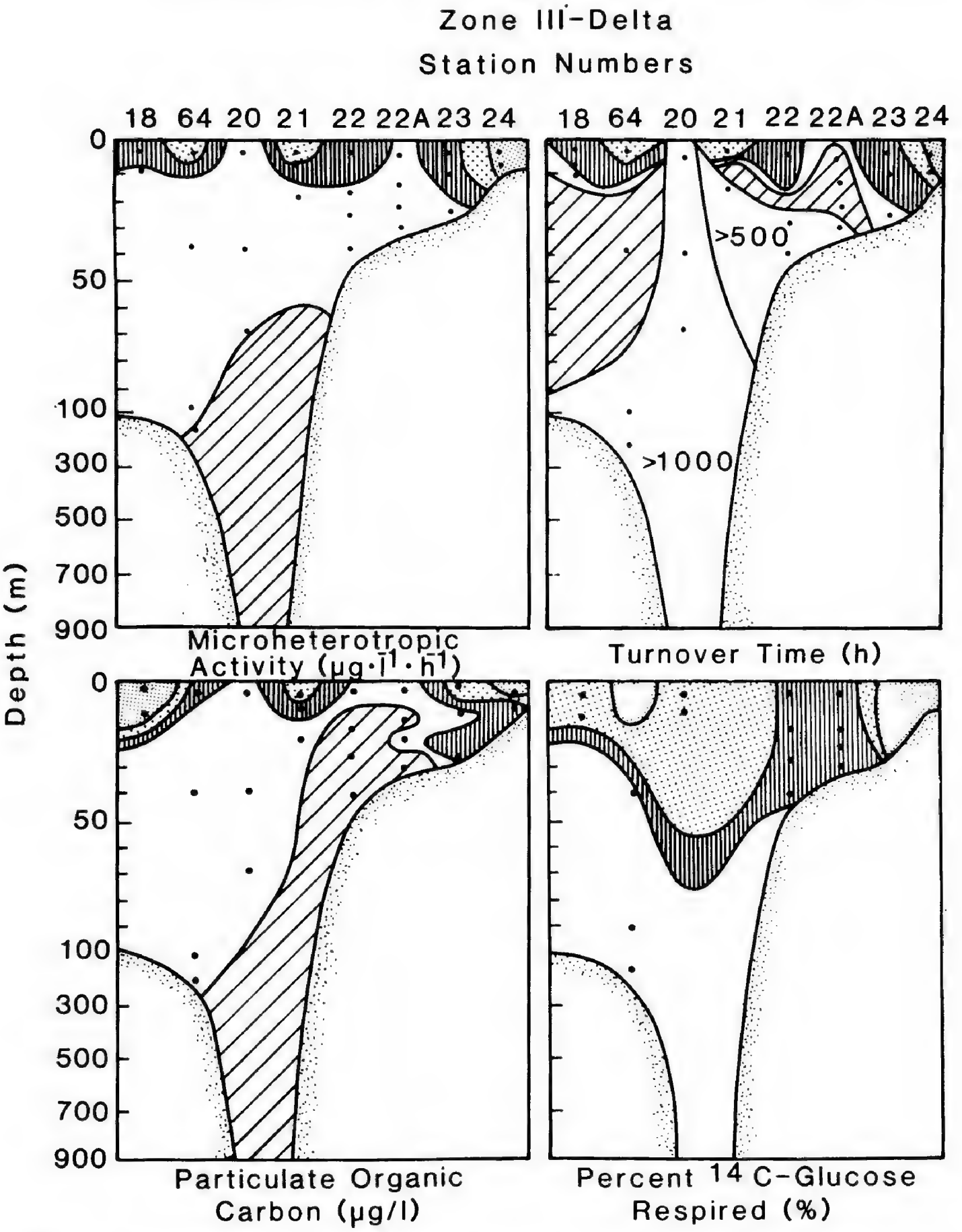


FIG. 5. Microheterotrophic activity, turnover time for the measured glucose, percentage of labeled glucose respired and particulate organic carbon concentrations in Zone III—Delta.

6). Highest microheterotrophic activity was in surface waters near the southwest entrance of the River. Microheterotrophic activity in most Gulf of Mexico waters was lower than found nearshore. Turnover times varied from less than 10 hours in the surface-nearshore waters to over 500 hours in

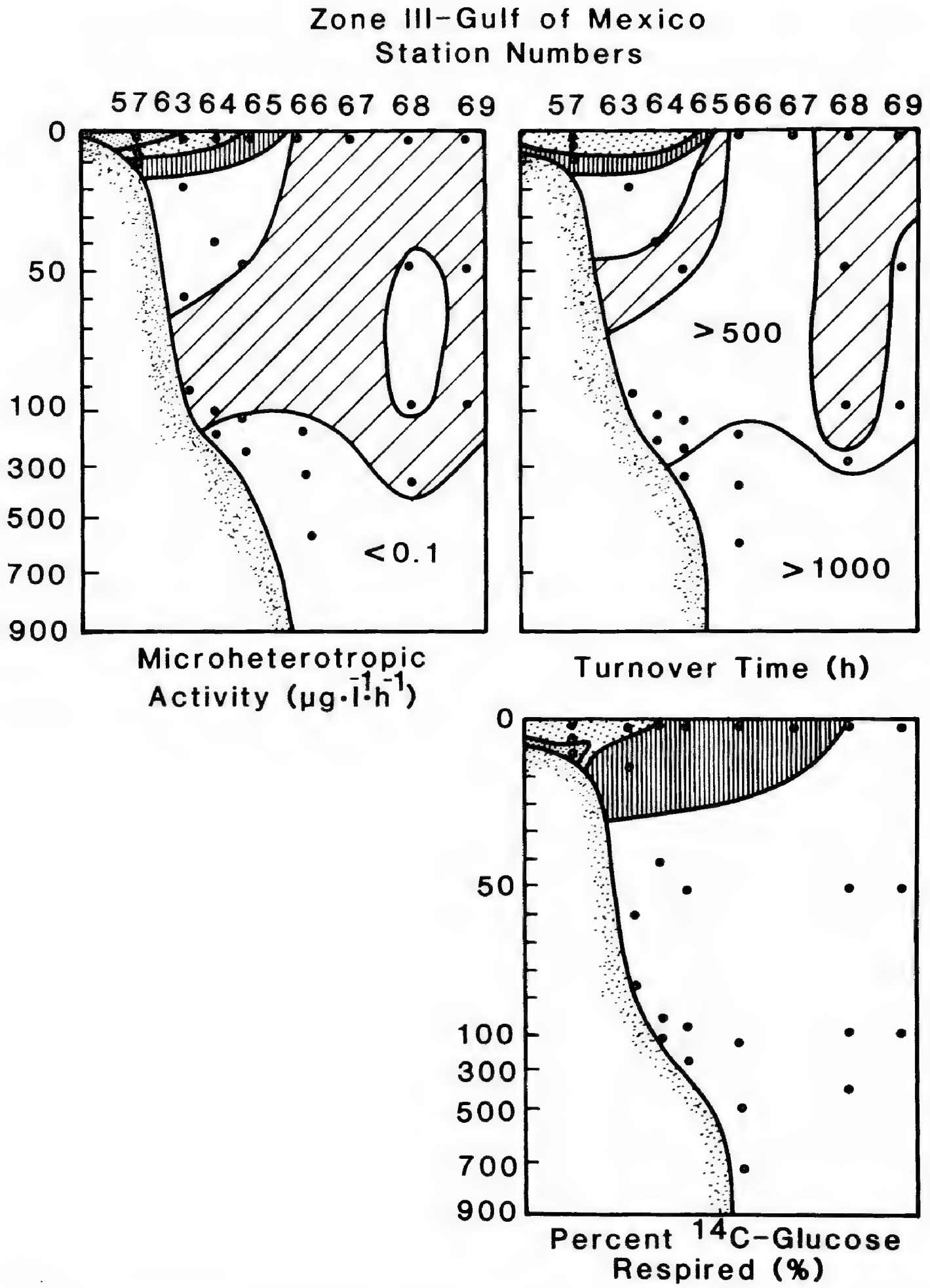


FIG. 6. Microheterotrophic activity, turnover time for the measured glucose, percentage of labeled glucose respired and particulate organic carbon concentrations in Zone III—Gulf of Mexico.

surface-offshore waters. Values for percent respired decreased from 20–30% in nearshore to 10–20% in offshore waters. Percentages respired in deep waters were between 2 and 10%. POC concentrations were not determined along this transect.

Microheterotrophic activity again coincided with salinity and temperature (Fig. 9). Highest activity was found in 20‰ waters even though surface-water temperatures remained at 23°C.

**Zone IV—Mississippi River Plume.** Most microheterotrophic activity greater than 1 μg/l·h was in surface waters of Mississippi River Plume (Fig. 7 + 8). Highest activity was in the plume's periphery and directly out from the southwest entrance (Station 49, 50 and 60). Turnover times were constant (5 to 10 hours) in surface waters but generally increased with depth. Values for percent respired glucose were highest (30–40%) in the plume's periphery. Highest POC concentrations (100–500 μg/l) were found in surface waters and centered around the River's outflow. Subsurface waters possessed relatively low POC concentrations (50 to 100 μg/l).

Hydrographic data collected within the plume area (Fig. 10) indicated that low salinity waters (15 to 30‰) had the highest values for microheterotrophic activity and POC. Highest values for percent respired were in waters with temperatures between 20 and 23°C.

## DISCUSSION

Estimates of microheterotrophic activity in Mississippi Delta Bight waters are reported. The results provide a picture of the spatial distribution of microheterotrophic activity within several zones seasonally influenced by the Mississippi River discharge.

This study will not be compared with other studies of microheterotrophic activity for several reasons. First, although the uptake of labeled glucose was linear for 5 hours for a coastal population, the reaction rate of an offshore population was exponential, which suggested that growth or the activity of offshore populations changed during the 6-hour assay. Thus, rates measured offshore probably overestimated activity relative to those measured nearshore. In spite of overestimation, however, the offshore rates were 10 to 100 times lower than those nearshore and within the Mississippi River Plume. The offshore populations appeared inactive or dormant, a feature common to oceanic bacterial populations (Novitsky and Morita 1977, Stevenson 1978, Wright 1979).

Second, respiration (percent of the total uptake of [$^{14}$C] glucose) decreased with time of incubation and did not stabilize until about 6 hours. A plausible explanation for some of the decrease in percent respiration is the loss of pool [$^{14}$C] carbohydrates as a result of acid-formaldahyde fixation. Therefore, the longer a sample is incubated the more time there is to fix [$^{14}$C] glucose into polymers and other cellular components. Consequently, for nearshore populations (incubation 2 hours), the apparent percent respired would be higher than those offshore (incubation 6 hours). How-

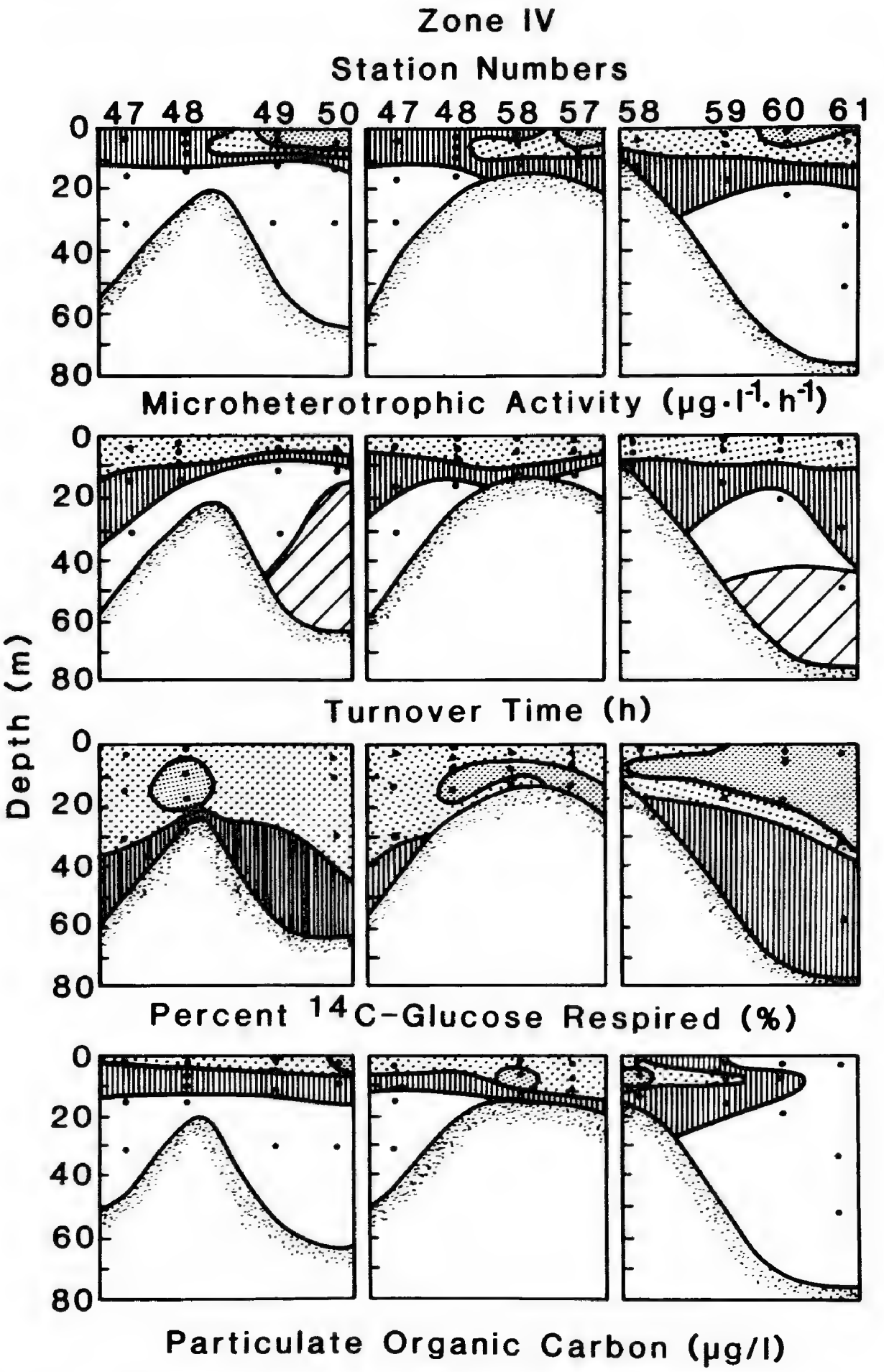


FIG. 7. Microheterotrophic activity, turnover time for the measured glucose, percentage of labeled glucose respired and particulate organic carbon concentrations in Zone IV—Mississippi Plume.

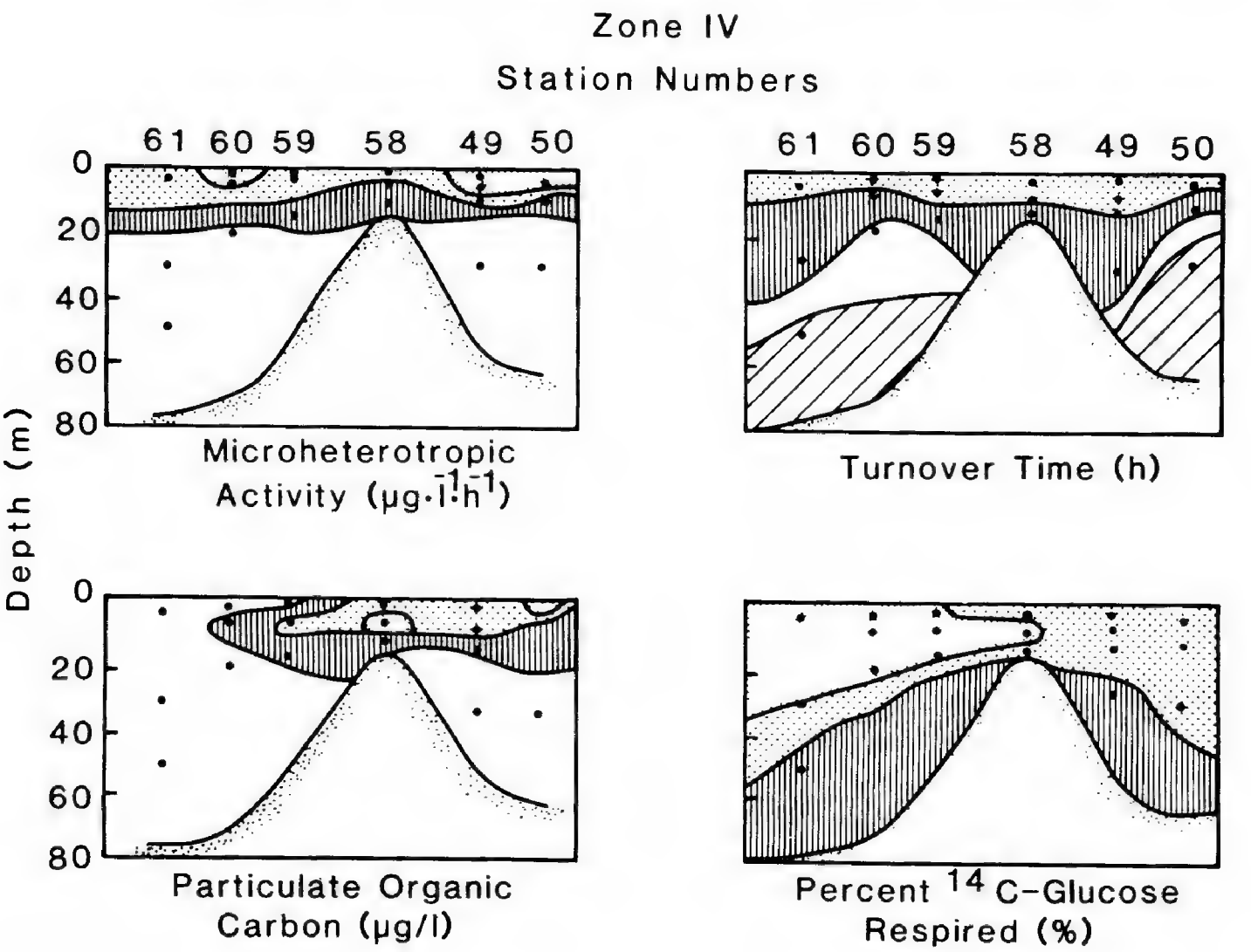


FIG. 8. Microheterotrophic activity, turnover time for the measured glucose, percentage of labeled glucose respired and particulate organic carbon concentrations in Zone IV—Mississippi Plume.

ever, at any one location vertical differences in the percentages respired are comparable. The relative decrease with increasing depth in percent respired is a function of the metabolic activity of the microheterotrophs.

Third, microheterotrophic activity was assessed by measuring the uptake of labeled [$^{14}$C] glucose. The rate of uptake is dependent on the concentration of natural glucose and other carbohydrates (Wood 1973, Wright 1973). Labeled [$^{14}$C] glucose was added to all samples at a concentration of 3 µg/l, or 10 to 100 times below reactive carbohydrate concentrations (Table 1). Therefore, the labeled glucose was a minute (trace) amount of the reactive carbohydrates and should not have enhanced microheterotrophic activity. However, if natural glucose concentrations were low ($<$ 10 µg/l or less) the uptake of labeled glucose would be affected and the uptake of the added glucose would not be at tracer concentration.

Finally, glucose concentrations in the Mississippi Delta Bight were estimated by an enzymatic measurement (Hicks and Carey 1968). After the samples were analyzed we discovered that the assay may overestimate glucose concentrations by 50% in marine waters (Hanson and Snyder, 1979a). Fructose interferred most with the glucose assay. Recently, Mopper

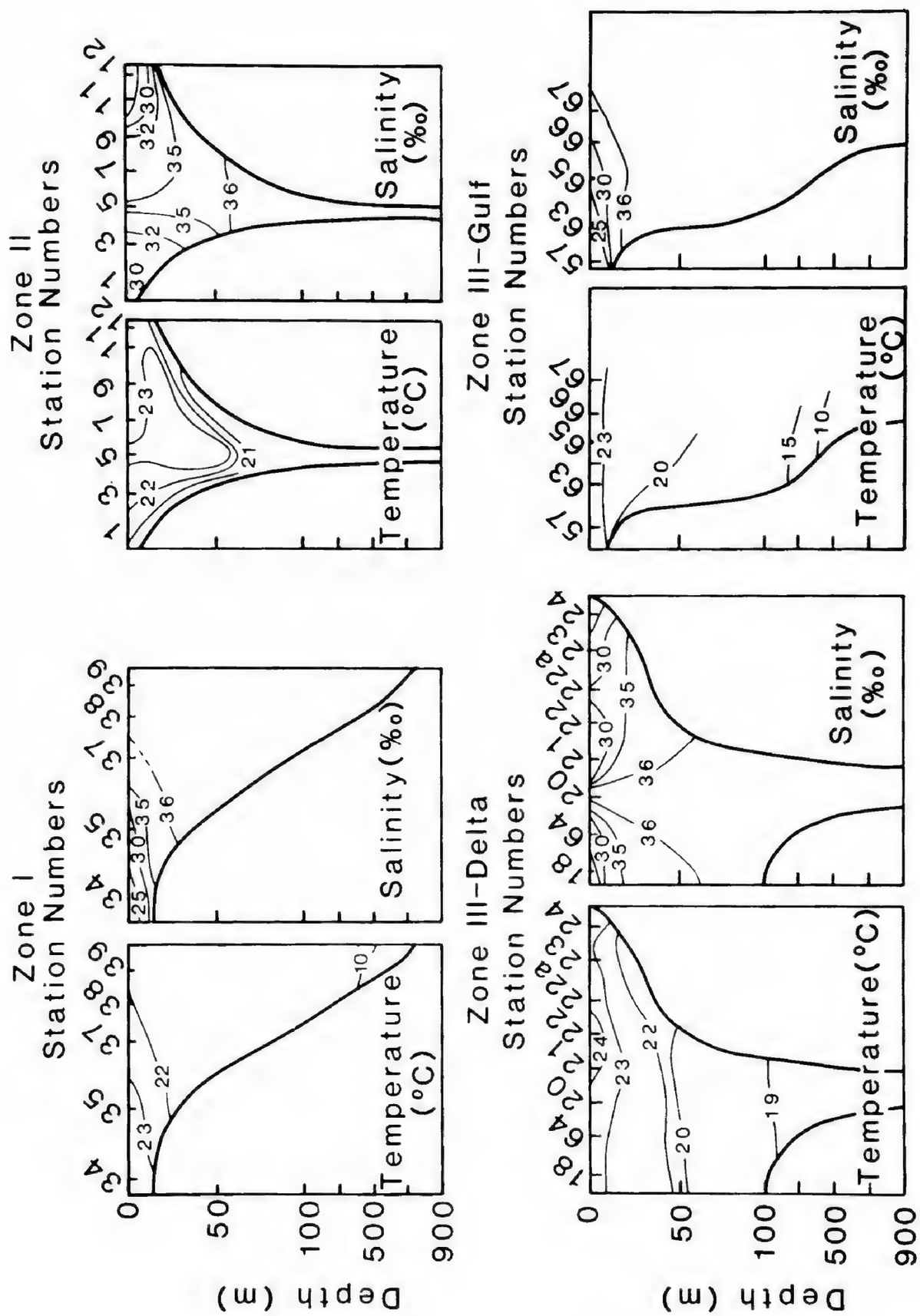


FIG. 9. Temperature and salinity isopleths in Zones I, II, III—Delta, and III—Gulf of Mexico.

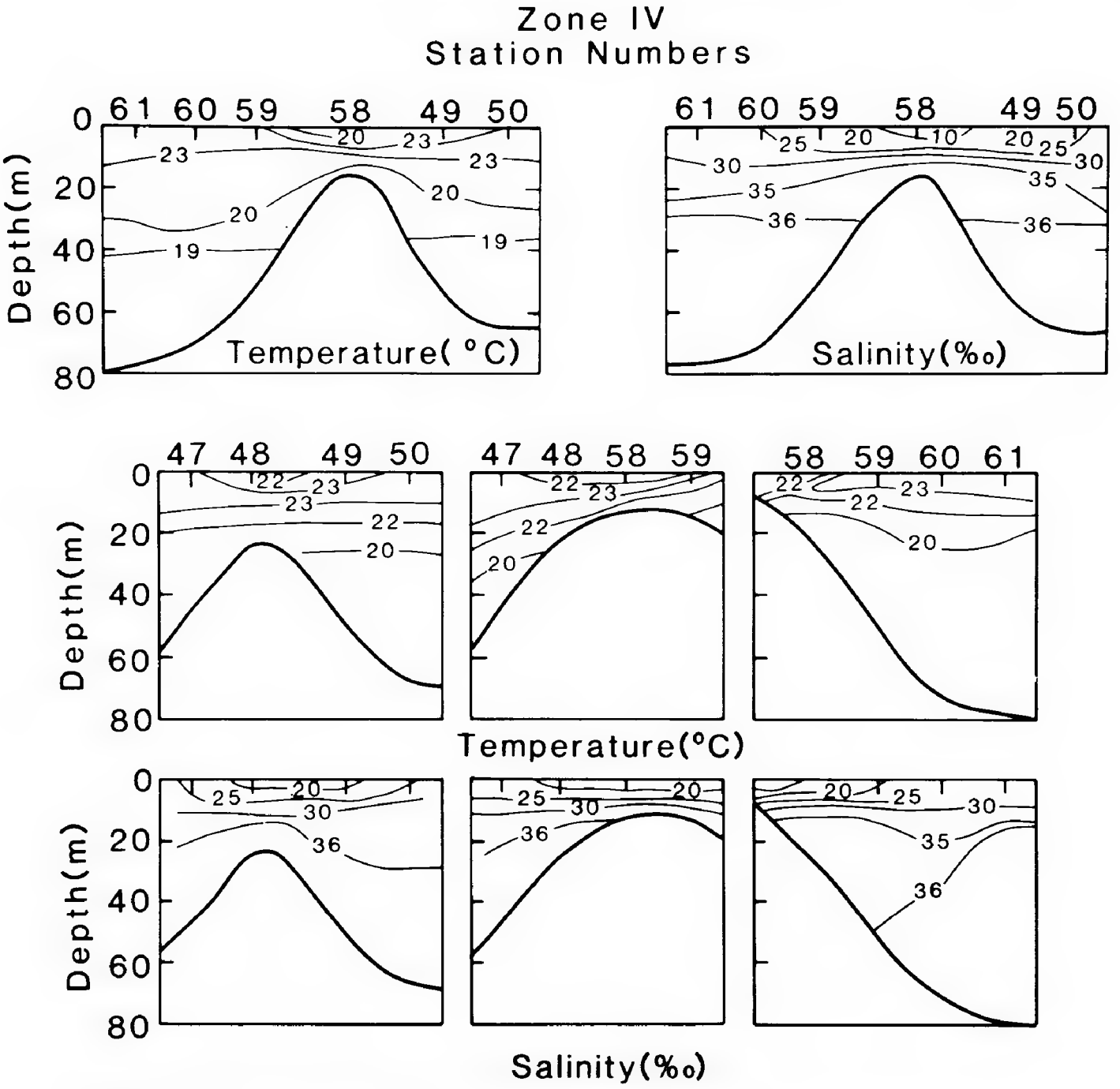


FIG. 10. Temperature and salinity isopleths in Zone IV—Mississippi Plume.

*et al.* (1980) reported that the ratio of fructose to glucose in natural waters usually ranges between 1.0 and 1.4:1, and the ratio is independent of the concentration of total monosaccharides. In many marine environments, more than 60% of the free, dissolved carbohydrate pool is comprised of glucose followed by fructose, mannose, galactose, and xylose (Ittekkot *et al.* 1981). We do not know the concentration of fructose in the Mississippi Delta Bight. Instead of correcting glucose values for fructose interference by entering an unknown factor in the calculations, values from the Hicks and Carey method are reactive carbohydrates but expressed as glucose. Natural concentrations would only approach these values if all of the reactive carbohydrates were present as glucose. Even though our results show that reactive carbohydrate concentrations were between 30 and 100 μg/l, we do not know how much of this carbohydrate pool was available to micro-heterotrophs. The concentration of carbohydrates obtained by chemical

analysis may not be totally available to microheterotrophs (Gocke *et al.* 1981, Hanson *et al.* 1982a).

Most productive waters occur along coasts and near continental shelf breaks (Wangersky 1977). Often, the productivity of oceanic waters correlates with the concentration of particulate organic carbon (POC). Major sources of POC in coastal areas are from terrestrial runoff and river outflow (allochtonous material) and autochthonous material resulting from nutrient enrichments and phytoplankton production. In the Mississippi Delta Bight POC concentrations in surface waters were between 100 and 700 μg/1 and the highest values occurred in low salinity (about 20‰) water which suggest that the Mississippi River is the major source of POC.

Like other indices of productivity, microheterotrophic activity coincided with concentrations of particulate organic carbon. High microheterotrophic activity is frequently found in waters with high POC and DOC (Albright and Wentworth 1973, Albright 1977, Hanson and Wiebe 1977, Fuhrman *et al.* 1980) and suspended solids (Bent and Goulder 1981). In some areas particulates may be major sites for microbial attachment and activity (Paerl 1974, 1975; Hanson and Snyder 1980). The actual site (*e.g.*, free-floating or associated with particulates) of microheterotrophic activity was not assessed in this study. However, in turbid salt-marsh estuaries, 80 to 90% of the activity is usually retained by 3-μm filters (Hanson and Wiebe 1977; Hanson and Snyder 1979b, 1980). This evidence suggests that in turbid waters with high concentrations of particulate organic carbon, such as the Mississippi River Plume, most active microheterotrophs would be attached to particulates. In the Mississippi River Delta high activity coincided with high POC and suggested that microheterotrophs were associated with particulates. In oceanic waters, on the other hand, particulates are scarce and frequently lack microbes (Wiebe and Pomeroy 1972). In such areas most of the activity (90%) passes through 3-μm filters (Azam and Hodson 1977, Hanson and Wiebe 1977, Hanson *et al.* 1982b) which suggests that measured activity is due to free-floating microheterotrophs.

In summary, the spatial distribution of microheterotrophic activity is related to distance from shore and the position of Mississippi River outflow. Highest activity occurred in waters with high POC concentrations and low salinity whereas the activity decreased with distance offshore and with water depth in the Gulf of Mexico.

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## LITERATURE CITED

ALBRIGHT, L. J. 1977. Heterotrophic bacterial dynamics in the lower Frazer River, its estuary and Georgia Strait, British Columbia, Canada. *Marine Biology.* 39:203–211.

———— and J. W. WENTWORTH. 1973. Use of the heterotrophic activity technique as a measure of eutrophication. *Environmental Pollution.* **5**:59–72.

ALEXANDER, S. K. and J. R. SCHWARZ. 1980. Short-term effects of south Louisiana and Kuwait crude oils on glucose utilization by marine bacterial populations. *Applied and Environmental Microbiology.* **40**:341–345.

ALLEN, R. L. and R. E. TURNER. 1977. Mississippi Delta Bight Studies No. 5, Hydrographic Data: April 27–May 9, 1977. Louisiana State University Center for Wetland Resources, Baton Rouge, LA. Sea Grant Publ. No. **LSU-SG-TL-77-005** (t). Microfiche.

AZAM, F. and R. E. HODSON. 1977. Dissolved ATP in the sea and its utilization by marine bacteria. *Nature.* **267**:696–698.

BENT, E. J. and R. GOULDER. 1981. Planktonic bacteria in the Humber Estuary; seasonal variation in population density and heterotrophic activity. *Marine Biology.* **62**:35–45.

FUHRMAN, J. A., J. W. AMMERMAN and F. AZAM. 1980. Bacterioplankton in the coastal eutrophic zone: distribution, activity and possible relationships with phytoplankton. *Marine Biology.* **60**:201–207.

GOCKE, K., R. DAWSON and G. LIEBEZEIT. 1981. Availability of dissolved free glucose to heterotrophic microorganisms. *Marine Biology.* **62**:209–216.

GOLDBERG, E. D. 1971. River-ocean interactions. pp. 143–156. In Costlow, J. D. (ed.) *Fertility of the Sea,* Gordon and Breach, New York.

GRAVINE, R. W. 1974. Physical features of the Connecticut River outflow during high discharge. *Journal of Geophysical Research.* **79**:831–846.

———— and J. D. MONK. 1974. Frontal structure of a river plume. *Journal of Geophysical Research.* **79**:2251–2259.

GRIFFITHS, R. P., F. J. HANUS and R. Y. MORITA. 1975. The effects of various water-sample treatments on the apparent uptake of glutamic acid by natural marine microbial populations. *Canadian Journal of Microbiology.* **20**:1261–1266.

HANSON, R. B. and W. J. WEIBE. 1977. Heterotrophic activity associated with particulate size fractions in a *Spartina alterniflora* Loisel. salt-marsh estuary, Sapelo Island, Georgia and the continental shelf waters. *Marine Biology.* **42**:321–330.

———— and J. SNYDER. 1979a. Enzymatic determination of glucose in marine environments: improvement and note of caution. *Marine Chemistry.* **7**:353–362.

———— and J. T. SNYDER. 1979b. Microheterotrophic activity in a salt-marsh estuary, Sapelo Island, Georgia. *Ecology.* **60**:99–107.

———— and J. SNYDER. 1980. Glucose exchanges in a salt-marsh estuary: biological activity and chemical measurements. *Limnology and Oceanography.* **25**:633–642.

————, G. SANTIAGO and A. PEREZ. 1982a. Effects of upwelling on microheterotrophic activity in the Rias of NW Spain. *Marine Ecology, Progress Series.* (submitted).

————, H. K. LOWERY, D. SHAFER, R. SORRACO and D. H. POPE. 1982b. Bacterioplankton productivity in the Drake Passage, Antarctica. *Deep-Sea Research.* (submitted).

HICKS, S. E. and F. G. CAREY. 1968. Glucose determination in natural waters. *Limnology and Oceanography.* **13**:361–363.

HOBBIE, J. E. and C. C. CRAWFORD. 1969. Respiration correction for bacterial uptake of dissolved organic compounds in natural waters. *Limnology and Oceanography.* **14**:528–532.

ITTEKKOT, W., U. BROCKMANN, W. MICHAELIS and E. T. DEGENS. 1981. Dissolved free and combined carbohydrates during a phytoplankton bloom in the northern North Sea. *Marine Ecology, Progress Series.* **4**:299–305.

MOPPER, K., R. DAWSON, G. LIEBEZEIT and V. ITTEKKOT. 1980. The monosaccharide spectra of natural waters. *Marine Chemistry.* **10**:55–66.

NOVITSKY, J. A. and R. Y. MORITA. 1977. Survival of a psychrophilic marine vibrio under long-term nutrient starvation. *Applied and Environmental Microbiology.* **33**:635–641.

OUJESKY, H., W. BROOKS, B. SMITH and B. HAMILTON. 1979. Water column bacteriological studies of the south Texas and continental shelf. *Developments in Industrial Microbiology.* **20**:695–703.

PAERL, H. W. 1974. Bacterial uptake of dissolved organic matter in relation to detrital aggregation in marine and freshwater systems. *Limnology and Oceanography.* **19**:966–972.

———. 1975. Microbial attachment to particles in marine and freshwater ecosystems. *Microbial Ecology.* **2**:73–83.

STEVENSON, L. H. 1978. A case for bacteria dormancy in aquatic systems. *Microbial Ecology.* **4**:127–133.

STRICKLAND, J. D. H. and T. R. PARSONS. 1972. A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board of Canada.* No. **167**. 311 pp.

VACCARO, R. F. and H. W. JANNASCH. 1966. Studies of heterotrophic activity in seawater based on glucose assimilation. *Limnology and Oceanography.* **11**:596–607.

WANGERSKY, P. J. 1977. The role of particulate matter in the productivity of surface waters. *Helgoländer Wissenschaftliche Meeresuntersuchungen.* **30**:546–564.

WIEBE, W. J. and L. R. POMEROY. 1972. Microorganisms and their association with aggregates and detritus in the sea: a microscopic study. *Memorie dell'Istituto Italiano di Idrobilogia.* **29** Suppl.: 325–352.

WOOD, L. W. 1973. Monosaccharide and disaccharide interactions on uptake and catabolism of carbohydrates by mixed microbial communities. pp. 181–197. In Stevenson, H. L. and R. R. Colwell (eds.), *Estuarine Microbiol Ecology,* Vol. 1, University of South Carolina Press, Columbia, South Carolina.

WRIGHT, R. T. 1973. Some difficulties in using $^{14}$C-organic solutes to measure heterotrophic bacterial activity. pp. 199–216. In Stevenson, H. L. and R. R. Colwell (eds.), *Estuarine Microbial Ecology,* Vol. 1, University of South Carolina Press, Columbia, South Carolina.

———. 1979. Measurement and significance of specific activity in heterotrophic bacteria of natural waters. *Applied and Environmental Microbiology.* **36**:297–305.

——— and J. E. HOBBIE. 1965. The uptake of organic solutes in lake water. *Limnology and Oceanography.* **10**:22–28.